In compliance with the
Canadian Privacy Legislation
some supporting forms
may have been removed from
this dissertation.

While these forms may be included
in the document page count,
their removal does not represent
any loss of content from the dissertation.

University of Alberta

SPATIO-TEMPORAL MOVEMENT AND ROAD CROSSING PATTERNS OF WOLVES, BLACK BEARS AND GRIZZLY BEARS IN THE BOW RIVER VALLEY OF BANFF NATIONAL PARK

by

Melanie P. Percy

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree Master of Science

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Fall 2003

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisisitons et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-87858-9
Our file Notre référence
ISBN: 0-612-87858-9

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou aturement reproduits sans son autorisation.

Canada

University of Alberta

Library Release Form

Name of Author: Melanie P. Percy

Title of Thesis: Spatio-temporal movement and road-crossing patterns of wolves, black bears and grizzly bears in the Bow Valley of Banff National Park

Degree: Master of Science

Year this Degree Granted: 2003

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.

Date: June 27, 2003

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Spatio-temporal Movement and Road-Crossing Patterns of Wolves, Black Bears and Grizzly Bears in the Bow Valley of Banff National Park** submitted by Melanie P. Percy in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

Date: June 26/2003

ABSTRACT

I monitored the daily movement patterns of radio-collared wolves (*Canis lupus*), black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos*) in the Bow Valley of Banff National Park between 1998 and 2001 to determine when they travel through wildlife corridors, areas of high human-use, and across roads. I examined the relationship between road-crossing frequency and hourly traffic volume for each species, and used binary logistic regression modelling to determine spatial and temporal characteristics of road-crossings events.

Wolves moved primarily during daylight and twilight in winter and during night and twilight in spring and summer. Black and grizzly bears were mainly crepuscular and diurnal. Wolves only traveled through areas of high human-use during winter nights, but used wildlife corridors during all daylight periods. Both black and grizzly bears used wildlife corridors primarily at night and during crepuscular hours.

Road-crossing frequency was negatively correlated with hourly traffic volume for all three species, although black and grizzly bears still continued to cross roads when traffic volumes were high. Wolves and grizzly bears showed an increase in their use of one or more spatial security features at road-crossing sites as traffic volume increased. I suggest that spatial and temporal movement patterns of wolves and bears are influenced by human use of the valley. I recommend temporal closures of secondary roads, restricting human use of wildlife corridors and limiting off-trail recreation to increase habitat effectiveness for large carnivores in the Bow Valley.

ACKNOWLEDGEMENTS

This project would not have been possible without the support, dedication and advice of a great number of people. I thank Parks Canada, the Friends of Banff National Park, the University of Alberta, the NSERC Discovery Grant (awarded to Suzanne Bayley), the Central Rockies Wolf Project, the Eastern Slopes Grizzly Bear Project, and the Paquet Fund for Wildlife Conservation for supporting my project, either financially or logistically.

I extend great thanks to my supervisor, Suzanne Bayley, for her guidance and support throughout my thesis, and to my committee members Colleen C. St. Clair and Fiona Schmiegelow for always being eager to offer their expertise and advice. Paul Paquet was instrumental in developing project ideas and provided many years of wisdom and expertise on large carnivore issues in Banff. I am grateful to Tony Clevenger, who was a key influence during the inception of the study, and shared ideas and expertise regarding field methods and study design.

Tom Hurd and Cliff White of Banff National Park provided invaluable advice, feedback and support throughout all stages of the project. I thank National Park Wardens Tom Davidson, Alan Dibb, Mike Gibeau, Jim Mammalis, Steve Michel, Hal Morrison, Dave Norcross, Joe Owchar and Glen Peers for field and logistical support throughout the project and during bear-trapping operations. Darrel Zell provided invaluable GIS expertise and advice, for which I am extremely grateful.

Todd Shury, D.V.M. assisted with black and grizzly bear care during trapping and gave excellent advice on wildlife care and handling. Charles Mamo led the bear-trapping efforts, teaching me the ins and outs of bear handling - I truly feel that I learned from the best.

I am grateful to the excellent team of dedicated field technicians that assisted me with data collection: Steve Anderson, Jennifer Grant, Laura Holmes, Lori Homstol, Danielle Robertson, Lisa Tedesco, and especially to Erin Urton, who assisted with field operations and managed the project while I was fulfilling course requirements in Edmonton. My thanks also to Mark Edwards, Robbie Gareau, Otso Huitu, Timm Kaminski, Joachim Vos, and Jennifer Wasylyk who devoted time to monitoring my study animals while working on other projects in the valley.

I feel incredibly fortunate to have worked within a team of enthusiastic, dedicated wildlife ecologists during my years in Banff, many of whom have become dear friends. I thank Shelley Alexander, Gunther and Karin Bloch, Carolyn Callaghan, Brenda Dobson, Danah Duke, Mike Gibeau, Mark Hebblewhite, Tom Hurd, Barb Johnston, Melissa Mauro, Bridget McClarty, Cedar Mueller, Rhonda Owchar, Joanne Saher, Saundi Stevens, Cliff White and Jesse Whittington for much support and inspiration throughout my work. I would especially like to thank Carolyn Callaghan for her wisdom, guidance and friendship, and for providing me with my first opportunity to work with wolves in Banff.

During the data analysis process, Cam Aldridge, John Brzustowski, Mark Hebblewhite, Scott Nielsen, Markus Thorman and Nigel Waltho provided valuable advice for which I am very appreciative.

I am eternally grateful to my family for always believing in me and inspiring me to follow my heart, no matter how tough the challenges or obstacles along the path. And to Steve Michel, my partner, best friend, and rock of stability, thank you for providing all the love, support, comic relief, patience and understanding that was instrumental in retaining my sanity throughout this process. To Beau, Daisy, Emily and Misko, thank you for your unconditional love, positive energy and devoted canine companionship that allow me to frequently escape the human world and remember what's really important in life.

Finally, I thank my study animals - those still with us and those whose lives have been lost. They have been my greatest inspiration throughout the last four years, and will live forever in my memory.

TABLE OF CONTENTS

CHAPTER 1: GENERAL INTRODUCTION 1

INTRODUCTION 1
PURPOSE AND OBJECTIVES 3
LITERATURE CITED 6

CHAPTER 2: SPATIO-TEMPORAL PATTERNS OF WOLF, BLACK BEAR AND GRIZZLY BEAR ROAD CROSSING EVENTS IN THE BOW VALLEY OF BANFF NATIONAL PARK 8

INTRODUCTION 8
STUDY AREA 12
METHODS 15
Field Methods 15
GIS, Spatial and Temporal Data 17
Statistical Analysis 20
Road Crossing Patterns of Wary vs. Human-Habituated Black Bears 20
Road Crossing Frequency Relative to Season and Daylight 21
Relationship between Hourly Traffic Volume and Road-Crossing Frequency 22
Multivariate Logistic Regression Modelling 22
RESULTS 26
Road Crossing Patterns of Wary vs. Human-Habituated Black Bears 26
Road Crossing Frequency Relative to Season and Daylight 27
Relationship Between Hourly Traffic Volume and Road Crossing Frequency 29
Multivariate Logistic Regression Modelling 29
Wolves 31
Black Bears 31
Grizzly Bears 32
Temporal Road-Crossing Patterns of the Bow Valley Parkway 33
DISCUSSION 34
Wolves 34
Black Bears 37
Grizzly Bears 40
CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS 42
LITERATURE CITED 46
APPENDIX 1 63
APPENDIX 2 64
APPENDIX 3 65

CHAPTER 3: TEMPORAL MOVEMENT PATTERNS OF WOLVES, BLACK BEARS AND GRIZZLY BEARS IN THE BOW VALLEY OF BANFF NATIONAL PARK 67

INTRODUCTION 67
STUDY AREA 70
METHODS 72
Field Methods 72
GIS, Spatial and Temporal Data 74
Statistical Analysis 75
RESULTS 77
Daily Movement Patterns 77
Wolves 77
Wary Black Bears 81
Habituated Black Bears 82
Grizzly Bears 84
Temporal Movement Patterns around Wildlife Corridors and Areas of High Human Use 86
Wolves 86
Black Bears 87
Grizzly Bears 88
DISCUSSION 88
Wolves 88
Black Bears 92
Grizzly Bears 94
Study Limitations 95
CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS 96
LITERATURE CITED 99

CHAPTER 4: THE EFFICIENCY OF USING RADIO TELEMETRY TO ESTIMATE WOLF ROAD-CROSSING LOCATION AND FREQUENCY **110**

INTRODUCTION 110
STUDY AREA 111
METHODS 112
Estimation of Road-Crossing Frequency 114
Estimation of Road-Crossing Location 114
RESULTS 116
Road-Crossing Frequency 116
Road-Crossing Location 116
DISCUSSION 117
LITERATURE CITED 119

CHAPTER 5: GENERAL CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS **124**

LITERATURE CITED 127

LIST OF TABLES

Table 2-1: Summary of road crossings by radio-collared wolves, black bears and grizzly bears in the Bow Valley of Banff National Park, May 1998 to March 2001 53

Table 2-2: Spearmans Correlation Matrix of Spatial and Temporal Road-Crossing Variables 53

Table 2-3: Results of Mann-Whitney U tests comparing use of BVP road-crossing variables by habituated versus non-habituated black bears. 54

Table 2-4: Results of matched-case control logistic regression examining differences between actual and estimated spatial road-crossing attributes 54

Table 2-5: Top set of wolf models for BVP crossing events. 54

Table 2-6: Averaged beta coefficients, standard errors and relative importance of variables in averaged BVP wolf crossing model 55

Table 2-7: Prediction Success Table for averaged wolf road crossing model. 55

Table 2-8: Top set of black bear models for BVP crossing events 55

Table 2-9: Averaged beta coefficients, standard errors and relative importance of variables in averaged BVP black bear crossing model. 56

Table 2-10: Prediction Success Table for averaged black bear road crossing model. 56

Table 2-11: Top set of grizzly bear models for BVP crossing events. 56

Table 2-12: Averaged beta coefficients, standard errors and relative importance of variables in averaged BVP grizzly bear crossing model. 57

Table 2-13: Prediction Success Table for averaged grizzly bear road crossing model. 57

Table 3-1: Hourly movement rates of radio-collared wolves, black bears and grizzly bears relative to daylight class. 104

Table 4-1: Number of wolf road crossings detected with six temporal resolutions of radio-telemetry. 121

Table 4-2: Median and mean error (m) of wolf road crossing locations estimated from radio telemetry conducted at six temporal intervals. 121

LIST OF FIGURES

Figure 2-1: Map of the greater Banff National Park region illustrating the study area.....58

Figure 2-2: Wolf crossing frequency of the Bow Valley Parkway relative to hourly traffic volume class.....59

Figure 2-3: Black bear crossing frequency of the Bow Valley Parkway relative to hourly traffic volume class.....59

Figure 2-4: Grizzly bear crossing frequency of the Bow Valley Parkway relative to hourly traffic volume class.....60

Figure 2-5: Hourly frequency of Bow Valley Parkway crossings by wolves in Banff National Park.....61

Figure 2-6: Hourly frequency of Bow Valley Parkway crossings by black bears in Banff National Park.....62

Figure 2-7: Hourly frequency of Bow Valley Parkway crossings by grizzly bears in Banff National Park.....62

Figure 3-1: Map of the greater Banff National Park region illustrating the study area.....105

Figure 3-2: Hourly movement rates (m) of wolf M1 and wolf M2 in the Bow Valley of Banff National Park.....106

Figure 3-3: Hourly movement rates (m) of wary black bears in the Bow Valley of BNP 107

Figure 3-4: Hourly movement rates (m) of human-habituated black bears in the Bow Valley of BNP.....108

Figure 3-5: Hourly movement rates (m) of grizzly bears in the Bow Valley of BNP 109

Figure 4-1: Map of the greater Banff National Park region illustrating the study area.....122

Figure 4-2: Mean error distance of road crossing locations estimated with radio telemetry conducted at increasing temporal intervals.....123

CHAPTER 1

GENERAL INTRODUCTION

INTRODUCTION

High levels of human activity throughout the central Rocky Mountain ecosystem have resulted in significant fragmentation of wildlife habitat, a reduction in habitat effectiveness, disturbance of predator/prey relationships, direct mortality and shifts in habitat-use patterns, ultimately posing a significant threat to the persistence of wildlife populations. Although physical fragmentation plays an important role in habitat loss and alienation, the mere presence of humans may displace sensitive wildlife species from otherwise effective habitat.

Large carnivores are particularly sensitive to the effects of habitat fragmentation and human disturbance due to their low population densities, low fecundity, wide-ranging habits, large home ranges, and wariness of humans (Noss et al. 1996; Weaver et al. 1996; Carroll et al. 2000). In theory, national parks and other protected areas should function as core refugia for large carnivores. However high levels of vehicular traffic, recreation and commercial activity jeopardize the wildlife these areas are mandated to protect. In recent years, Parks Canada has recognized the issue of habitat fragmentation, habitat loss and species decline in areas of Banff National Park (BNP), particularly the Bow River Valley. The Bow Valley contains a disproportionately high percentage (77.4%) of BNP's montane

habitat, considered the most productive habitat for wolves, grizzly bears and black bears (Kansas et al. 1989; Gibeau et al. 1996; Paquet et al. 1996). A significant reduction in habitat effectiveness has occurred in the Bow Valley as a result of a high-speed transportation network, abundant commercial development and high levels of human use (Paquet et al. 1994; Gibeau et al. 1996; Paquet et al. 1996). The valley is now considered a potential fracture zone to large carnivore movements and genetic exchange in the central Rocky Mountains (Servheen et al. 1998), and an area where the long term prospect for large carnivore viability is considered poor (Paquet et al. 1996; Gibeau 2000). To restore habitat effectiveness and increase habitat security for large carnivores in the Bow Valley, Parks Canada must devise innovative human-use strategies, balancing human use of the landscape with wildlife requirements.

In the presence of high levels of human activity, large carnivores may select habitat with higher vegetative security cover to remain cryptic to humans, they may shift their activity patterns to avoid habitat at times when human use is high, or they may completely abandon habitat resulting in localized extinction (Griffiths and Van Schaik 1993). The severity of the response may depend on the level of disturbance and the behavioural plasticity of the individual animal or species. To accurately determine the effects of human activity on large carnivores, habitat use and movement studies should incorporate nocturnal as well as diurnal data collection (Beyer and Haufler, 1994). Once baseline spatial and temporal activity patterns are determined, they can be used to gauge impacts of ecosystem change

on wildlife (Roth 1983). A number of studies in BNP have addressed habitat use of large carnivores, but few have incorporated a fine-scale temporal element.

PURPOSE AND OBJECTIVES

The purpose of my thesis is to examine the spatio-temporal movement patterns of wolves (*Canis lupus*), black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos*) in the Bow Valley of Banff National Park, and to document movement patterns across roads, through designated wildlife corridors, and through areas of high human use.

In Chapter 2, "Spatio-Temporal Patterns of Wolf, Black Bear and Grizzly Bear Road-Crossing Events in the Bow Valley of Banff National Park", I used radio-telemetry to examine the spatio-temporal road crossing patterns of wolves and bears. My specific objectives were to:

(1) Test whether road-crossing behaviour is consistent between wary and human-habituated black bears;

(2) Test whether the road-crossing frequency of wolves, black bears and grizzly bears varies with human-use season and daylight;

(3) Examine the relationship between hourly traffic volume and road-crossing frequency of the three focal species;

(4) Examine the importance of spatial and temporal variables associated with wolf, black bear, and grizzly bear road crossings using predictive multivariate logistic regression models;

(5) Determine temporal patterns in wolf, black bear and grizzly bear crossings of a major secondary road (the Bow Valley Parkway) to guide the development of temporal travel restrictions;

(6) Recommend management actions to increase habitat effectiveness around roads for wolves, black bears and grizzly bears in the Bow Valley of Banff National Park.

In Chapter 3, "Temporal Movement Patterns of Wolves, Black Bears and Grizzly Bears in the Bow Valley of Banff National Park", I used radio-telemetry monitoring to study the daily movement patterns of wolves, black bears and grizzly bears. The specific objectives of Chapter 3 were to:

1) Test whether the movement patterns of wolves, black bears and grizzly bears change throughout the 24-hour day and between seasons;
2) Test whether wolf movement patterns during denning/rendezvous season are influenced by the presence of pups;
3) Test whether differences exist in the daily movement patterns of wary versus human-habituated black bears;
4) Test whether wolves, black bears, and grizzly bears use wildlife corridors and areas of high human-use through time relative to the surrounding landscape.

In Chapter 4, "The Efficiency of Using Radio-telemetry to Estimate Wolf Road Crossing Location and Frequency", I critically assessed the use of radio-telemetry in estimating road-crossing frequency and location for wolves. I used six temporal resolutions of telemetry and snow tracking data to determine how length of time between consecutive telemetry data acquisition influences estimation of road-crossing frequency and location.

In Chapter 5, I provide general conclusions and recommendations as to how Parks Canada can allow human use in the Bow Valley while restoring habitat effectiveness for large carnivores.

LITERATURE CITED

Beyer, D.E. and J.B. Haufler. 1994. Diurnal versus 24-hour sampling of habitat use. *J. Wildl. Manage*. 58(1): 178-180.

Carroll, C., P.C. Paquet, and R.F. Noss. 2000. Modeling Carnivore Habitat in the Rocky Mountain Region: A Literature Review and Suggested Strategy. World Wildlife Fund, Toronto, Ontario. 104pp.

Gibeau, M.L., S. Herrero, J. Kansas, and B. Benn. 1996. Grizzly Bear Population and Habitat Status in Banff National Park. Chapter 6 in: Green, J., C. Pacas, L. Cornwell and S. Bayley (eds). Ecological Outlooks Project. A Cumulative Effects Assessment and Futures Outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, ON. 52 pp.

Gibeau, M.L. 2000. A Conservation Biology Approach to Management of Grizzly Bears in Banff National Park, Alberta. Ph.D. Dissertation, University of Calgary, Alberta.

Griffiths, M. and C.P. Van Schaik. 1993. The impact of human traffic on the abundance and activity periods of Sumatran rainforest wildlife. *Cons. Biol*. 7(3): 623-626.

Kansas, J.L., R.M. Raine, and M.L. Gibeau. 1989. Ecological Studies of the Black Bear in Banff National Park, Alberta. 1986-1988. Final Report.

Noss, R.F., H. Quigley, M. Hornhocker, T. Merrill, and P. Paquet. 1996. Conservation biology and carnivores: conservation in the Rocky Mountains. *Cons. Biol*. 10: 949-963.

Paquet, P.C., J. Wierzchowski, and C. Callaghan. 1996. Effects of Human Activity on Gray Wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 in: Green, J., C. Pacas, L. Cornwell and S. Bayley (eds.). Ecological Outlooks Project. A Cumulative Effects Assessment and Futures Outlook for the Banff Bow Valley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, ON. 74 pp.

Paquet, P.C., M.L. Gibeau, S. Herrero, J. Jorgenson, and J. Green. 1994. Wildlife Corridors in the Bow River Valley, Alberta: A Strategy for Maintaining Well Distributed, Viable Populations of Wildlife. A report to the Bow River Valley Corridor Task Force. Canmore, Alberta. 37 pp.

Roth, H.U. 1983. Diel activity of a remnant population of European brown bears. *Int. Conf. Bear Res. and Manage.* 5: 223-229.

Servheen, C., J. Waller, and W. Kasworm. 1998. Fragmentation effects of high speed highways on grizzly bear populations shared between the United States and Canada. p. 97-103 in: Evink, G.L., D. Zeigler, and J. Berry, eds. Proceedings of the International Conference on Wildlife Ecology and Transportation. FL-ER-69-98, Florida Department of Transportation, Tallahassee, Florida. 263pp.

Weaver, J., P.C. Paquet, and L. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Cons. Biol.* 10: 964-976.

CHAPTER 2

SPATIO-TEMPORAL PATTERNS OF WOLF, BLACK BEAR AND GRIZZLY BEAR ROAD CROSSING EVENTS IN THE BOW VALLEY OF BANFF NATIONAL PARK

INTRODUCTION

Habitat fragmentation, resulting in the loss and isolation of effective wildlife habitat, is widely recognised as a leading cause in the loss of biodiversity (Wilcox and Murphy 1985; Saunders et al. 1991; Davies et al. 2001). Roads represent a significant form of habitat fragmentation, and may effectively block wildlife movement across natural home ranges, reducing ecological connectivity and threatening the persistence of sub-populations (Gilpin and Soulé 1986; Forman et al. 2002). Bennett (1981), Jalkotzy et al. (1997), and Trombulak and Frissel (2000) provide comprehensive reviews of the effects of roads on wildlife.

Large carnivores are known to be particularly sensitive to the effects of roads and other sources of habitat fragmentation due to their low population densities, low fecundity, wide-ranging habits, large home ranges, and wariness of humans (Noss et al. 1996; Weaver et al. 1996; Carroll et al. 2000). Landscapes with road densities exceeding 0.6 km/ km^2 (0.93 miles/$mile^2$) may fail to support wolf populations (Thiel 1985; Jensen et al. 1986; Mech 1988), and selection for

habitats with lower road density has also been documented for bobcat (Lovallo and Anderson 1996), grizzly bear (Mattson et al. 1987; McLellan and Shackleton 1988; Mace et al. 1996; Mace et al. 1999), and black bear (Brody and Pelton 1989).

Traffic levels may play a greater role in the habitat avoidance exhibited by many carnivores than does road density, as roads themselves do not prevent carnivores from inhabiting an area. Rather, roads increase human access that, in turn, may displace sensitive carnivores. Carnivores have been shown to reduce habitat use surrounding roads and to cross roads less often as traffic volume increases (Archibald et al. 1987; Mattson et al. 1987; McLellan and Shackleton 1988; Beringer et al. 1990; Brandenburg 1996; Lovallo and Anderson 1996; Mace et al. 1996; Serrouya 1999; Gibeau 2000; Alexander 2001). Such negative associations may result in the disruption of foraging activity, thereby lowering survival and fecundity (Mattson et al. 1987).

The lure of roads and road right-of ways as movement corridors (Mech 1970; Thurber et al. 1994; Brandenburg 1996; Paquet et al. 1996; James 1999) and as potential sources of forage (Gibeau and Herrero 1998), may result in a dynamic tension between carnivore attraction to and repulsion from roadside environments (Brody and Pelton 1989; Gibeau and Hererro 1998). Naturally wary individuals may become alienated from critical habitat (Kasworm and Manley 1990; Paquet et al. 1996; Gibeau 2000) and those individuals whose attraction to roadside

resources outweighs the perceived disturbance by humans may become habituated to human activity (Archibald et al. 1987). In both cases, the result is a loss of habitat effectiveness, with human-habituated individuals being at greater risk of dying on roads or in confrontations with humans (Archibald et al. 1987; Gibeau 2000; Hebblewhite et al. 2003).

Even in protected areas, such as national parks, it may be necessary for large carnivores to cross busy roads on a daily basis to access food resources, den sites and mates. Banff National Park in the Canadian Rocky Mountains represents such a protected area. The high speed Trans Canada Highway bisects the park through the Bow River Valley, forming one of a number of potential fracture zones to large carnivore movements and genetic exchange in the central Rocky Mountains (Servheen et al. 1998). In recent years, Parks Canada has recognised the issue of habitat fragmentation, habitat loss and species decline, specifically within the Bow Valley. As park visitation levels and traffic volumes are projected to increase in future years (Pacas 1996), Parks Canada must devise innovative human-use strategies to improve habitat effectiveness and habitat connectivity for large carnivores. Such strategies may include temporal management of traffic along secondary roads, construction of continuous landscape overpasses across roadways, and general human-use quotas.

Although a number of studies have assessed the impacts of roads on large carnivore habitat use, few have addressed the effect of hourly traffic volume or

time of day on large carnivore road-crossing patterns (Brandenburg 1996; Percy et al. 1998; Gibeau 2000). Furthermore, no study has investigated the impacts of hourly traffic volume and level of daylight on wildlife selection of spatial attributes at road-crossing sites. Temporal patterns in the differential use of spatial features at crossing sites may indicate a disturbance response to increasing levels of traffic and a reduction in road permeability.

The objectives of my research were: (1) to test whether road-crossing behaviour is consistent between wary and human-habituated black bears; (2) to test whether road-crossing frequency of wolves, black bears and grizzly bears varies with human-use season and daylight; (3) to examine the relationship between hourly traffic volume and road-crossing frequency of wolves and bears; (4) to examine the importance of spatial and temporal variables associated with wolf, black bear, and grizzly bear road crossings using multivariate logistic regression modelling; (5) to determine temporal patterns in wolf, black bear and grizzly bear crossings of a major secondary road (the Bow Valley Parkway) to assist in planning temporal travel restrictions; and (6) to recommend management actions to increase habitat effectiveness adjacent to roads for wolves, black bears and grizzly bears in the Bow Valley of Banff National Park.

STUDY AREA

The study was conducted between May 1998 and March 2001 in the Bow Valley of Banff National Park. Banff park is located between 120 and 200 kilometres west of the city of Calgary, Alberta, Canada, in the Front and Main ranges of the Canadian Rocky Mountains. The park is approximately 6640 km^2 in area and is characterised by rugged mountainous topography. Within Banff, the Bow Valley extends from the park east gate, located approximately 10 km west of the town of Canmore, Alberta, to its headwaters at Bow Lake, located approximately 35 km NNW of the village of Lake Louise. The valley ranges from approximately two to six kilometres in width, is oriented on a NW to SE axis, and has valley-bottom elevations ranging from approximately 1330 to 2000 metres. The study area also extends west of the town of Lake Louise to Kicking Horse Pass near the Alberta/British Columbia border, and includes the northern portion of the Vermilion watershed from Castle Junction to Marble Canyon in Kootenay National Park, B.C (Figure 2-1).

Steep mountains and ridges create natural fragmentation of the landscape, while the infrastructure required to accommodate more than five million visitors per year (Cornwell et al. 1996) has subjected the valley to extensive human-induced fragmentation.

Habitat within the study area is classified as belonging to the montane, subalpine or alpine ecoregion (Holland and Coen 1983) depending on elevation. Vegetation is dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), poplar (*Populus sp.*) and Douglas fir (*Pseudotsuga menziesii*) forests, grassy slopes, shrubby wetland complexes, and alpine meadows. In addition to wolves, black bears and grizzly bears, large terrestrial fauna found within the study area include elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemonius*), bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*), moose (*Alces alces*), wolverine (*Gulo gulo*), cougar (*Puma concolor*), lynx (*Felis lynx*) and coyote (*Canis latrans*). Climate is characterised by long, cold winters, and relatively short, dry summers.

Four major transportation corridors lie within the study area: the Trans Canada Highway (TCH), the Canadian Pacific Railway, Highway 93, and the Bow Valley Parkway (BVP). During the study period, daily traffic volumes for the TCH ranged from 3,400 to over 22,000 vehicles per day, and hourly volume ranged from 8 to 2,630 vehicles per hour. The BVP ranges in daily traffic volume from 55 to over 3,500 vehicles, with hourly traffic volumes ranging from zero to over 400 vehicles per hour, depending on time of year. Highest traffic volumes occur during the months of July and August, and lowest volumes occur in November and January (Banff National Park, unpublished data). Highway 93 ranges in traffic volume from 55 to over 7,000 vehicles per day (Banff National Park,

unpublished data). The westernmost 35 km of the TCH is two lanes wide and unfenced, while the balance of the TCH within the study area is four lanes wide and bounded by 2.4 metre high wildlife exclusion fencing. To increase highway permeability, 24 wildlife crossing structures and bridges (22 underpasses and 2 overpasses) were constructed during highway expansion to facilitate wildlife movement across the highway (Clevenger and Waltho 2000).

During the study period, Parks Canada experimented with a voluntary travel restriction along the easternmost 17 kilometres of the BVP between Johnston Canyon and Five Mile bridge, just west of the town of Banff. Travel was discouraged between the hours of 18:00 and 09:00 from March 1 through June 25 (in all years of the study), in an effort to increase habitat effectiveness for wildlife along the parkway. The efficacy of the travel restriction at reducing traffic volume was negligible. During the closure months, traffic volume decreased by approximately 17% on the restricted portion of the parkway. However, it is important to note that there was an overall annual decrease in traffic volume by 14% on this stretch of road for years when the closure was implemented, which coincides with the completion of highway upgrades to the adjacent section of the TCH in 1997 (Parks Canada, unpublished data). Field observations also suggest compliance for the travel restriction was low. Signage for the restriction was poor, the road was not gated, nor was the restriction enforced.

METHODS

Field Methods

I monitored two wolves from two different packs (alpha male, Bow Valley Pack; adult male, Fairholme Pack), eighteen black bears (11 male [9 adult, 2 subadult]; 7 female [6 adult; 1 subadult]) and three grizzly bears (1 adult male; 2 adult female) equipped with conventional VHF radio collars (Lotek Engineering, Newmarket, Ontario). Wolves were captured in modified steel foot-hold traps (toothed and padded No. 4 offset foot-hold traps, Livestock Protection Co., Alpine, TX), immobilised with a tiletamine hydrochloride/zolazepam hydrochloride mixture (Telazol™ at 5 mg/kg), and fitted with VHF radio-collars. Black and grizzly bears were captured in steel culvert traps, mesh guillotine traps, or in Aldrich foot snares using natural bait, immobilised with Telazol™ (4-6 mg/kg for black bears, 7-9 mg/kg for grizzly bears), or with a Telazol™/Xylazine (Rompun™) mixture (2mg/kg:1mg/kg for black bears, 3 mg/kg:1mg/kg for grizzly bears) administered intramuscularly via jab stick or projectile dart. Ketamine hydrochloride (Ketaset™, 2mg/kg) was used to lengthen or deepen anaesthesia, if necessary.

To obtain data on road-crossing patterns, I located radio-collared wolves, black bears and grizzly bears using conventional radio-triangulation (White and Garrott 1990) conducted from accessible roads in the study area. I determined observer location with the use of a hand-held global positioning system (GPS) unit

(Garmin 12XL, Garmin International Inc.), plotted telemetry bearings on 1:20,000 geo-corrected air photos, and recorded animal locations in UTM co-ordinates. I assessed average telemetry error by conducting conventional triangulation on stationary test collars placed between 300 metres and 1.5 km from roads in the study area. Average error was approximately ±150 metres, consistent with other telemetry-based research in Banff National Park (Serrouya 1999; Gibeau 2000; Hebblewhite 2000; Callaghan 2002).

Approximately three times per week, I conducted continuous 24-hour radio-telemetry monitoring sessions, focusing on one to three animals per session. I obtained one grizzly bear or black bear location every two hours, and one wolf location every hour for at least 24 consecutive hours. I relocated wolves more frequently as they typically travel faster than bears. I terminated a monitoring session if the focal animal moved out of telemetry range and more than one scheduled location was missed. If an animal was visually observed crossing a road during the monitoring session, I recorded the exact crossing location with a GPS unit. During winter months, I confirmed wolf road crossings detected during 24-hour monitoring sessions with tracks in snow, and recorded the exact crossing location with a GPS unit. Tracks were only recorded as actual crossing locations when I could be certain that they were those of the collared animal.

GIS, Spatial and Temporal Data

I converted animal locations to spatial GIS (Geographic Information System) files using Arcview 3.2 (ESRI Inc., Redlands, CA.), and superimposed a digital road layer of the study area onto the animal location files. Using Arcview 3.2, I drew straight-line trajectories between consecutive telemetry locations within a given monitoring session, and inferred a road crossing when consecutive locations occurred on opposite sides of a road. I considered the point at which the straight-line trajectory intersected the road to be the "estimated" road crossing location. Crossing locations confirmed by visual observation of the animal or its tracks were considered "actual" crossing locations.

Time of road crossing was estimated as the mid-point between the time of location x_i and the time of location x_{i+1}, when the two locations occurred on opposing sides of the road. Accuracy of this method was within one hour for black and grizzly bears, and within one half hour for wolves. If a road crossing was visually observed during a 24-hour monitoring session, the actual crossing time was used.

I constructed digital layers for six spatial habitat attributes at estimated and actual road crossing sites using ArcView 3.2: (1) drainage distance (distance in metres to the nearest drainage); (2) human-use distance (distance in metres to the closest area of high human use such as town sites, high-use trail heads, outlying

commercial accommodations etc.); (3) low-use linear feature distance (distance in metres to the nearest low or non-use anthropogenic linear feature such as powerlines, old road beds, gated railway access roads); (4) vegetative security cover; (5) terrain roughness; and (6) road curvature. I calculated all distance measurements as the straight-line distance between the crossing site and the nearest edge of the feature. For vegetative security cover and terrain roughness, I first constructed rectangular buffer zones extending 150 metres along the road on either side of each crossing location (to account for telemetry error) and 50 metres back from the road (to ensure I captured roadside attributes only). I calculated the percent vegetative security cover within each buffer zone using a binary-coded vegetation layer built from Indian Satellite data (Banff National Park, unpublished data), distinguishing trees, medium and large-sized shrubs (coded 1) from low shrubs, grass, pavement and water (coded 0). For terrain roughness, I used a digital elevation model to calculate the surface area and the flat area of each buffer zone and calculated terrain roughness with the formula:

$$\text{Terrain Roughness} = \text{Absolute Value}\,[(1-(\text{surface area}/\text{flat area}))*100]$$

I calculated the degree of road curvature within a 250-metre distance of each road-crossing location by placing a point 250-metres along the road on either side of a crossing location using GIS. The straight-line distance between these two points was calculated (Straightness Value), with a value of 500 indicating a

perfectly straight section of road. I then calculated percent curvature of the crossing site with the formula:

$$\% \text{ Curvature} = (1-(\text{Straightness}/500))*100$$

I did not include relative habitat quality as a spatial variable in the analysis, as suitable fine-scale GIS layers were not available for the three focal species in this area.

I used two temporal variables in my analysis of road crossings. I obtained hourly traffic volume data for the BVP, the TCH, and Highway 93 (Banff National Park, unpublished data). In the case of missing records, I estimated traffic volume for a particular date and time by averaging the traffic volume for the same date and time for the year before and after the crossing event (approximately 20 % of total records were estimated). I determined daylight at the time of each crossing with the aid of sunrise/sunset tables (Herzberg Institute of Astrophysics, National Research Council, Victoria, B.C.). "Dawn" covered the two hour period extending from one hour before sunrise to one hour after sunrise; "day" occurred from one hour after sunrise to one hour before sunset; "dusk" occurred from one hour before sunset to one hour after sunset; and "night" occurred from one hour after sunset to one hour before sunrise.

I grouped dawn and dusk crossings into a "twilight" class, and then divided crossings into one of three ordinal daylight classes to coincide with increasing levels of light: night = 0; twilight = 1; and daylight = 2. Length of daylight varied between 7.88 and 16.58 hours, and night varied from 9.2 to 18.1 hours in length. Crepuscular periods varied by 14 minutes throughout the year, and for simplicity of analysis I did not account for this variation.

Statistical Analysis

Road Crossing Patterns of Wary versus Human-Habituated Black Bears

I divided black bear data into one of two behavioural classes based on expert opinion (field staff and National Park Wardens) of established bear behaviour around humans. I considered bears that were known to be shy around humans and were rarely seen to be "wary", and those that were used to being approached or harassed by humans to be "habituated" (Herrero 1985). To test whether road-crossing frequency differed between wary and habituated black bears, I compared the crossing frequencies of the two behavioural classes of black bears (#crossings/24-hour monitoring session) using the non-parametric Mann-Whitney U test (Zar 1999). I then divided black bear road crossings into primary and secondary road types and used the G-test for heterogeneity (Sokal and Rohlf 1995) to test whether crossing frequencies of primary and secondary roads were consistent between the two behavioural classes. I used a G-test for goodness of fit (Sokal and Rohlf 1995) to test whether there was a difference in frequency of

secondary road versus primary road crossings by black bears. I used 25 kilometre, parallel sections of the BVP (secondary road) and unfenced TCH (primary road) for this analysis. The two roads are approximately 800 metres apart throughout this portion of the valley.

Road-Crossing Frequency Relative to Human-use Season and Daylight

To test how the frequency of wolf, black bear and grizzly bear road crossings varied with human-use season and with daylight, I defined human use seasons as: Spring (April 1 to June 14), Summer (June 15 to September 14), Fall (September 15 to November 30), and Winter (December 1 to March 31), based on fluxes in park visitation. I compared road-crossing frequency across seasons, and across daylight classes (n = 4, see methods above) within seasons for each species using the G-test for goodness of fit with the Williams' correction factor for small sample sizes (Sokal and Rohlf 1995). The expected frequency of road crossings for each species in a given season was proportional to the number of 24-hour monitoring sessions during the season. This corrected for uneven sampling intensity across seasons. The expected number of road crossings per daylight class per season was proportional to the number of hours that each daylight period was available (Herzberg Institute for Astrophysics Sunrise/Sunset Tables, National Research Council, Victoria, B.C.). If any test resulted in a significant difference, I examined the G-test residuals to determine which daylight classes deviated most from expected (Sokal and Rohlf 1995). I set experiment-wise alpha levels at 0.10 to increase the ability to identify biologically meaningful differences.

Relationship between Hourly Traffic Volume and Road-Crossing Frequency

I examined the effect of hourly traffic volume on crossing frequency for each road separately due to the wide variation in traffic level between roads. Due to small sample sizes of Hwy 93 and TCH crossings, I performed this analysis for Bow Valley Parkway crossings only. I determined the range of hourly traffic volumes during which wolf, black bear and grizzly bear crossings occurred and divided traffic volume into 25 classes of ten vehicles per hour (vph) (i.e. Class 1 = 0 to 9 vph; Class 2 = 10 to 19 vph, etc.). I used Spearman's rank correlation coefficients (r_s) (Zar 1999) to examine the relationship between wolf, black bear and grizzly bear crossing frequency and hourly traffic volume class (SYSTAT Version 10.0, SPSS Inc. 2000).

Multivariate Logistic Regression Modelling

Prior to the multivariate analysis of road crossings, I used a Spearman's correlation matrix to determine co-linearity among continuous spatial and temporal predictor variables (SYSTAT Version 10.0, SPSS Inc. 2000). Any two spatial variables with a resulting correlation of >0.50 were considered correlated and were not included into the same multivariate model. Although daylight and hourly traffic volume may be naturally correlated due to the human active cycle, I retained both variables for multivariate analysis as each may have an important effect on road-crossing patterns.

Significant differences in habitat use and movement patterns may exist between habituated and wary animals due to their different comfort levels around humans and human facilities. I used a series of Mann Whitney U-tests to determine if there were differences in the use of each predictor variable at road-crossing sites by the two behavioural classes of black bears (SYSTAT Version 10.0, SPSS Inc. 2000). I did not perform this analysis for grizzlies due to the low sample size.

To determine whether road-crossing locations estimated from radio-telemetry data were sufficiently accurate to use in a multivariate road-crossing model, I tested for differences between "actual" road crossing locations and their respective telemetry-estimated crossing locations. I used a subset of 42 actual crossings that occurred between consecutive telemetry locations and paired each with a corresponding estimated location, determined using methods described above. To identify differences in spatial attributes of estimated and actual crossing sites I used a 1:1 matched-case control logistic regression analysis (SYSTAT Version 10.0, SPSS Inc. 2000) stratifying actual (as cases) and estimated (as control) crossing sites by crossing event (animal, date and time). In this use of case-control logistic regression, a non-significant beta coefficient for each spatial predictor variable was required to proceed with pooling estimated and actual road crossing data in subsequent multivariate analyses. More generally, one would use it to detect differences between cases and their controls (Hosmer and Lemeshow 1989).

I used multiple logistic regression to create spatio-temporal road-crossing models for wolves, black bears and grizzly bears, and to determine biologically important spatial and temporal variables associated with road-crossing events. I divided the data by species and by road and randomly generated two available crossing locations (i.e. control sites) per documented crossing (Manly et al. 1993) using ArcView 3.2. I ensured that the number of control sites for each road was proportional to the number of documented crossings of that road for each species. I generated all spatial variables for control sites as for road-crossing sites, and generated random dates and times for control sites (Excel, Microsoft Corp., 1997). I ensured that the proportion of control sites in each season reflected the crossing data for each species, to account for imbalances in monitoring intensity across seasons.

I used backward stepwise logistic regression on each main data set to select potentially meaningful variables for inclusion in multivariate models. I included all six spatial and two temporal variables in the stepwise procedure, in addition to seven second-order spatio-temporal interaction terms. Interaction terms address the differential selection for spatial attributes as level of a temporal attribute (light or traffic volume) changes. I used a backward variable selection procedure with an entry criteria of $P < 0.5$, and a removal criteria of $P < 0.25$. The threshold for variable inclusion was less stringent than the usual $P < 0.05$ to ensure the inclusion of biologically significant variables (Hosmer and Lemeshow 1989). Furthermore, models were assessed using an information theoretic approach (see

below) whereby the consideration of P values is generally avoided. In this case, I used liberal P values to reduce the number of single and second-order terms I included in multivariate models, as all terms were considered potentially meaningful. Variables showing significance at the $P < 0.25$ level were retained as predictor variables to be used in multivariate road-crossing models. The group of retained predictor variables was then used to develop a set of candidate models for each species for each road. I ran each candidate model using binary logistic regression (SYSTAT Version 10.0, SPSS Inc. 2000), and ranked each model relative to the other models in its set using Akaike's Information Criterion (AIC) for small sample sizes (AIC_c) (Burnham and Anderson 1998). Candidate models were ranked according to the change in AIC_c (ΔAIC_c) of each model from the model with the lowest AIC_c (top model). I determined the AIC weight of each model, and used a cumulative weight of 0.90 and a ΔAIC_c of <4.0 as criteria for selecting the "best" model/s (Burnham and Anderson 1998). In cases when there was more than one top model, I used a model averaging approach to account for model selection uncertainty (Burnham and Anderson 1998). I determined the 90% confidence limits for the resulting parameter estimates using the AIC weights. To determine the relative importance of the individual parameters, I examined the change in log-likelihood of the averaged model when an individual parameter was excluded.

To assess how well the AIC-averaged models fit the data, I used the Hosmer-Lemeshow goodness of fit test (Hosmer and Lemeshow 1989), and examined

McFaddens ρ^2 values and model prediction success tables (SYSTAT Version 10.0, SPSS Inc. 2000). McFaddens ρ^2 mimics a linear regression R^2 with values ranging between 0 and 1. The McFaddens ρ^2 however, gives much lower values than an R^2, with values in the 0.2 to 0.4 range indicating a very strong model (Tabachnik and Fiddell 2001).

RESULTS

A total of 249 24-hour monitoring sessions (117 wolf, 105 black bear, and 27 grizzly bear) yielded 403 road crossings, and thirty-eight additional road crossings were detected outside of the 24-hour monitoring sessions (Table 2-1). I detected fifty-seven crossings of the four-lane, fenced section of the TCH, which likely involved the use of wildlife crossing structures. These data were not considered, as an analysis of variables influencing the use of wildlife crossing structures was beyond the scope of this paper. Clevenger and Waltho (2000) report on the efficacy of wildlife crossing structures in Banff. Only one wolf (alpha male of the Bow Valley Pack) crossed the Bow Valley Parkway, Highway 93 north and south and the unfenced section of the TCH, therefore all analysis is limited to this wolf.

Road-Crossing Patterns of Wary versus Human-Habituated Black Bears

Field technicians and surveyed National Park Wardens agreed unanimously on the behavioural classification of black bears. Twelve of eighteen black bears were

considered "wary" of humans and six black bears were considered habituated to humans. I documented 62 road crossings by habituated black bears during 31 24-hour monitoring sessions, and 92 road crossings by wary black bears during 74 monitoring sessions. Habituated black bears crossed roads at a significantly higher rate than did wary bears ($U = 1486.5$, $n = 31,74$, $z = 2.39$; $P = 0.017$).

The frequency of primary road crossings relative to secondary road crossings was similar for wary and habituated black bears given a critical alpha of 0.05 ($G_H = 3.78$, df = 1, $P = 0.052$). Primary roads accounted for 17% of wary black bear crossings, and 31% of human-habituated black bear crossings. Given the closeness of the resulting P value to the critical value suggests that these differences may be important. All black bears crossed primary roads significantly less often than secondary roads ($G = 15.762$; df = 1; $P = 0.0001$).

Road Crossing Frequency Relative to Human Use Season and Daylight

When adjusted for sampling intensity, wolves showed no difference in road-crossing frequency across seasons ($G_{adj} = 2.29$, df = 3, $P = 0.514$). There was a significant difference in black bear road crossing frequency across seasons ($G_{adj} = 6.75$, df = 2, $P = 0.034$), with roads being crossed less often in spring than expected and more often in summer. There was a significant difference in grizzly bear road crossing frequency across seasons ($G_{adj} = 14.40$, df = 2, $P = 0.001$),

with fewer crossings during fall than expected, and more crossings during spring and summer.

Wolves crossed roads at night, twilight, and daytime in proportion to the availability of these light periods during the fall (G_{adj} = 0.79, df = 2, P = 0.674) and spring (G_{adj} = 1.92, df = 2, P = 0.383). There were significant differences in wolf use of daylight periods for crossing roads during winter (G_{adj} = 6.19, df = 2, P = 0.045). Twilight and daylight crossings were higher than expected, and night crossings were lower than expected. There were significant differences in wolf use of daylight periods for crossing roads during summer (G_{adj} = 15.96, df=2, P = 0.0003), with more crossings occurring at twilight than expected, and more crossings at night than expected. Daylight crossings were lower than expected.

There were significant differences in black bear use of daylight periods for crossing roads during fall (G_{adj} = 8.36, df = 2, P = 0.015) and summer (G_{adj} = 54.66, df = 2, P = 0.0001). In spring, black bears used daylight periods to cross roads as expected. In summer and fall, black bears crossed roads more often during daylight and less often at night.

During spring, grizzly bears crossed roads at night, twilight, and daytime in proportion to the availability of these light periods (G_{adj} = 2.13, df = 2, P = 0.345). In summer, however, there was a significant difference in the use of light periods for road crossings (G_{adj} = 7.52, df = 2, P = 0.023) as grizzly bears crossed

roads more often during daylight and less often at night. There were no recorded grizzly bear road crossings during fall.

Relationship Between Hourly Traffic Volume and Road-Crossing Frequency

Crossing frequency of the BVP was negatively correlated with traffic volume class for all three species (wolf: r_s = -0.660, n = 25, P = 0.001; black bear: r_s = -0.770, n = 25, P = 0.001; grizzly bear r_s = -0.397, n = 25, P = 0.054). Seventy-two percent of wolf crossings of the BVP (n = 118) occurred when traffic volumes were between zero and nine vehicles per hour, and 93% occurred when traffic volumes were lower than 30 vehicles per hour. Only two of 118 crossings occurred when traffic volumes exceeded 79 vehicles per hour (Figure 2-2). Black bear crossing frequency was also highest within the lowest traffic volume class (0 to 9 vph), however, black bears clearly continued to cross roads as traffic volumes increased (Figure 2-3). Similarly, although grizzly bear crossing frequency of the BVP was negatively correlated with hourly traffic volume, they also crossed when traffic volumes were high (Figure 2-4).

Multivariate Logistic Regression Modelling

All spatial and temporal variables were non-normally distributed. All spatial variables were non-correlated, however, the two temporal variables (daylight and traffic volume) were correlated (r_s = 0.705) (Table 2-2). I retained both temporal

variables in the multivariate analysis as each may have a different effect on road-crossing patterns.

Forty-two crossings of the BVP by habituated black bears and seventy-three crossings of the BVP by wary black bears were used to determine differences in road-crossing site selection between the two behavioural classes. Habituated and wary black bears showed no significant differences in their use of spatial or temporal road-crossing attributes (Table 2-3). However, habituated black bears tended to use crossing sites with higher curvature than did wary black bears (U = 1254.0; df = 1; P = 0.09) and this difference may have biological significance. Based on the statistical similarity of spatial and temporal predictor variables at crossing sites, BVP road-crossing data for habituated and wary black bears were consolidated for subsequent multivariate analyses.

There were no significant differences in the spatial attributes of estimated versus actual crossing locations (Table 2-4), therefore I consolidated estimated and actual crossings as case or "use" points in the subsequent logistic regression model.

Due to small sample size, I could not model crossings of Highway 93, and did not amalgamate these data with TCH crossings due to the wide variation in hourly traffic volume and spatial attributes of each road.

Wolves

Stepwise logistic regression yielded nine significant variables ($P < 0.25$) for inclusion in candidate wolf road-crossing models (Appendix 1). Twelve top models (Table 2-5) were averaged to create one "best" model for wolf crossings of the BVP (Table 2-6). Ambient light, security cover, and distance to human use were positively related to crossing probability, while traffic volume, distance to low/non use linear feature and terrain roughness were negatively related to crossing probability. Two spatio-temporal interaction terms were also positively related to crossing probability, light*security cover and light*curvature, while light*distance to human use was negatively related to crossing probability. Overall, light, traffic volume, distance to human use, and the distance to human use*light interaction term were the most important variables associated with wolf road-crossing probability (Table 2-6). The Hosmer-Lemeshow statistic for the averaged wolf model ($HL = 5.078$; df = 6; $P = 0.534$) suggests a relatively strong model (high P value indicates model strength with this statistic), while McFadden's ρ^2 statistic ($\rho^2 = 0.123$) and the model prediction success table (Table 2-7) indicate limitations to the model's strength and predictive ability.

Black Bears

Stepwise logistic regression yielded seven significant variables ($P < 0.25$) for inclusion in candidate black bear BVP crossing models (Appendix 2). Eight top models (Table 2-8) were averaged to create one "best" model for black bear crossings of the BVP (Table 2-9). Ambient light, distance to human use, and

traffic volume were positively related to black bear road-crossing probability, and terrain roughness was negatively related to crossing probability. Two spatio-temporal interaction terms were also positively related to crossing probability, traffic volume * light, and traffic volume * terrain roughness, while traffic volume*curvature was negatively related to crossing probability. Light and distance to human use were the highest-ranking variables in the model (Table 2-9). The Hosmer-Lemeshow statistic for the averaged black bear model (HL = 2.668; df = 5; P = 0.751) suggests a strong model (high P value), while the McFadden's ρ^2 statistic (ρ^2 = 0.116) and model prediction success table (Table 2-10) indicate limitations to the model's strength and predictive ability.

Grizzly Bears

Stepwise logistic regression yielded eight significant variables ($P < 0.25$) for inclusion in candidate grizzly bear road-crossing models (Appendix 3). Fourteen top models (Table 2-11) were averaged to create one "best" model for grizzly bear road crossings of the BVP (Table 2-12). Road curvature and security cover were positively related to crossing probability, and distance to low/non use linear feature was negatively related to crossing probability. The spatio-temporal interaction terms traffic volume * security, traffic volume * terrain roughness, and distance to human use * light were positively related to crossing probability while traffic volume * curvature, and light * security were negatively related to crossing probability. Examination of changes in log-likelihood upon parameter removal suggest that distance to human use * light, traffic volume * terrain roughness,

traffic volume * curvature, and distance to low/non-use linear feature were the most important variables in grizzly bear BVP crossing events (Table 2-12). The Hosmer-Lemeshow statistic for the averaged grizzly bear model (HL = 15.817; df = 8; P = 0.045) indicates a model with poor strength and predictive ability, however, the McFadden's ρ^2 statistic (ρ^2 = 0.286) and the model prediction success table (Table 2-13) indicate good predictive ability of the model.

The paucity of TCH data precluded a rigorous analysis of crossing events, therefore model results are not presented.

Temporal Road-Crossing Patterns of the Bow Valley Parkway

In spring, wolf crossings of the BVP (n = 19) peaked between 19:00 and 03:00. No crossings were documented between noon and 19:00. In summer, wolves crossed the BVP (n = 14) primarily between 22:00 and 06:00. No crossings occurred between noon and 23:00, and only 3 of 14 crossings occurred between 06:00 and noon. In fall, the majority of wolf crossings occurred between 14:00 and 22:00. All but three crossings (total n = 20) occurred between 07:00 and 22:00. In winter, wolves crossed the BVP throughout the day and night, with peaks occurring between 06:00 and 11:00, and between 14:00 and 21:00. Only 6 of 61 winter crossings were documented between midnight and 06:00 (Figure 2-2).

Black bear crossings of the BVP occurred throughout the day and night in spring, with only 2 of 13 crossings occurring between midnight and 06:00. In summer, peaks in black bear crossings of the BVP occurred between 09:00 and noon, and between 14:00 and 22:00. Only nine of 80 summer black bear crossings occurred during the late evening and early morning hours (22:00 to 07:00). In fall, black bears crossed roads predominantly during late morning, daytime, and early evening. Only two of eleven fall crossings occurred between 19:00 and 09:00 (Figure 2-3).

Grizzly bear crossings of the BVP during spring (n = 7) occurred primarily in the afternoon and early evening. Only one crossing occurred between 22:00 and 11:00. In summer, grizzly bear crossings of the BVP (n = 18) were distributed throughout the day and night, however there was a peak in crossing activity between 16:00 and 20:00. No grizzly bear crossings of the BVP were documented in fall (Figure 2-4).

DISCUSSION

Wolves

Wolves showed no difference in road-crossing frequency across calendar seasons. In spring and fall, wolves crossed the BVP with equal frequency in all daylight periods, but in winter they crossed less often at night, and in summer they rarely crossed during the day. During winter months, low daytime traffic volumes may

increase the permeability of the BVP. I observed wolves using the BVP and other low-use roads as travel corridors during daylight hours in winter months, a behaviour that has been well documented in BNP (Paquet et al. 1996; Alexander 2001; Bloch and Bloch 2002; Callaghan 2002) and in other study areas (Mech 1970; Thurber et al. 1994; James 1999; Whittington 2002). Conversely, high daytime traffic volumes on the BVP during summer months may create a temporal barrier to wolf movement across the Bow Valley.

Of the temporal variables, daylight had a positive influence on wolf road-crossing probability, while traffic volume had a negative effect. Wolf road-crossing sites were further from areas of high human use, closer to low/non-use linear features, and were characterised by higher vegetative security cover and flatter terrain than were randomly generated sites. The importance of vegetative security cover and road curvature at road-crossing sites increased as traffic volume increased. There was an inverse effect of distance to human use and level of daylight on wolf crossing probability, suggesting that wolves crossed roads closer to areas of high human use (less distance from high human use) when light levels were higher. This result may be a reflection of the high number of winter crossings that occurred close to areas characterised as generally high human use, but may in fact, receive very low human use during winter months.

Frair (1999) found that wolves in Wisconsin crossed highways where distance to opposite edge and road margin width were greater than found at random, and

crossings were unrelated to forest canopy cover. This finding differs from the positive effect of security cover in my model, and may be due to differences in wolf behaviour, or the possibility that the Wisconsin crossings may have occurred at night, or during very low traffic volumes when security may not be as important. Frair (1999) found that relative topography was not associated with crossing site selection, nor did wolves use trails to approach road-crossing sites. These findings also differ from mine as crossings in the Bow Valley were [illegible]iated with gentle terrain and were closer to old road beds, power lines and gated access roads, suggesting that wolves may use these features for travel.

Wolf road-crossing frequency was negatively correlated with traffic volume. Seventy-four percent of all crossings of the BVP occurred when traffic volumes were between zero and nine vehicles per hour, and only seven percent of all crossings occurred when traffic volumes exceeded 30 vehicles per hour. Thurber et al. (1994) also found a decrease in crossing frequency and use of roads as traffic volumes increased. In my study, wolf crossings of a secondary road (the BVP) occurred throughout the day and occasionally at night during fall and winter, however spring and summer crossings occurred exclusively between 19:00 and noon.

In summary, I found that wolves prefer to cross the BVP when traffic volumes are very low and during twilight or daylight. As traffic volumes increase, crossing

frequency decreases and crossings that do occur are associated with higher vegetative security and higher road curvature.

Black Bears

Black bears tended to cross roads more often during daylight than at night in all three seasons, and in summer, twilight crossings were more common than were night crossings. Beringer et al. (1990) also found that black bears in North Carolina crossed roads with higher frequency during daylight hours. This pattern may be indicative of the general diurnal movement pattern of black bears (Amstrup and Beecham 1976; Ayres et al. 1986; Lariviere et al. 1994).

Black bears that were habituated to human activity crossed roads significantly more often than did wary bears. Habituated black bears crossed primary roads more often than did wary black bears, however, crossings of secondary roads were significantly higher than crossings of primary roads for all black bears. Similarly, Brody and Pelton (1989), Beringer et al. (1990), Brandenburg (1996) and Serrouya (1999) found that black bears crossed secondary roads of lower traffic volume more frequently than higher-volume primary highways.

Black bear crossing frequency of the BVP was negatively correlated with traffic volume. Inverse relationships between traffic volume and road permeability to black bears have also been reported by Brody and Pelton (1989), Beringer et al.

(1990), Brandenburg (1996), and Serrouya (1999). In North Carolina, roads did not pose a barrier to black bear movement when traffic volumes were less than 100 vehicles per day (Beringer et al. 1990), whereas roads with high traffic volumes were crossed most often at night, or at times when traffic volumes were low (Beringer et al. 1990; Brandenburg 1996).

Black bear road-crossing events were more likely to occur during daylight, in more gentle terrain, and further from areas of high human use than randomly generated crossing events. As traffic volumes increased, black bears used crossing sites with higher terrain roughness, and lower road curvature than at random. The positive association with daylight and traffic volume may be more a function of black bear diurnal activity patterns than a lack of response to human use. An interesting result was the positive effect of traffic volume on black bear crossing frequency in the logistic regression model, which contradicts the negative correlation between traffic volume and crossing frequency. This discrepancy can be explained by the differences in the two statistical procedures. Logistic model development compared traffic volumes of black bear crossing events with events generated randomly through space and time. Randomly generated crossings undoubtedly had a higher nocturnal representation, and hence, lower traffic volumes than black bear crossing events, as black bears seem to be a primarily diurnal species in the Bow Valley. Correlation analysis was performed with hourly traffic volumes corresponding to actual black bear road-crossing events. There were fewer road crossings at higher traffic volumes than at

lower traffic volumes. It is likely that the unequal representation of nocturnal crossings in the logistic regression case and control data sets produced a positive effect of traffic volume on black bear road-crossing probability.

Vegetative security cover was not an important variable in my black bear road crossing model, however Brandenburg (1996) found that bears in North Carolina avoided habitat openings for crossing roads. These differing results may be due to the protected status of Banff bears, while Brandenburg's bears were from a hunted population and thus, may resort to more cryptic movement patterns. Distance to drainage was not a significant variable in my black bear road-crossing model, however, Brandenburg (1996) and Clevenger et al. (2002) found that black bear crossing sites were associated with drainages.

In spring, black bears showed no discernible temporal pattern in crossings of the BVP, with crossings occurring throughout the day, night and crepuscular hours. In summer, crossing frequency peaked in early to late morning and again in the evening, and in fall, the pattern was predominantly diurnal. Their preference for crossing roads during daylight hours may be more related to their diurnal activity pattern than their lack of response to human activity.

Grizzly Bears

Grizzly bears crossed roads with equal frequency during spring and summer, and I recorded no grizzly bear road crossings in fall. In spring, grizzlies crossed roads during daylight, night and twilight as expected, whereas in summer, grizzlies crossed roads more often during daylight than at night, with a peak in late afternoon and evening. Gibeau (2000) also noted a high number of grizzly bear road crossings during daylight hours. As with black bears, daylight crossings by grizzlies are likely the result of their diurnal activity patterns. There was a significant, negative relationship between traffic volume and grizzly bear crossing frequency of the BVP.

Grizzly bear crossing sites of the BVP had higher security cover and road curvature and were closer to low/non-use linear features than were randomly generated crossing sites. As traffic volumes increased, grizzlies used crossing sites with higher security cover, higher terrain roughness and lower road curvature than random. As ambient light increased, grizzlies crossed roads further from areas of high human use, and where security cover was lower than random. Although one would expect bears to use higher security cover for daylight crossings, the fact that two of three study bears were habituated may explain this result. Gibeau (2000) found that grizzly bear crossing "zones" along the BVP were characterised by low human access density (density of roads and hiking trails), were close to major drainages, in more rugged terrain, and in areas of

higher quality habitat. Road crossing sites inferred from this study are consistent with crossing zones identified by Gibeau (2000).

In summary, crossing frequency of the BVP by all three species was negatively related to traffic volume however black and grizzly bears continued to cross roads at higher traffic volumes while wolves did not. Current levels of traffic volume on the BVP may create a temporal barrier to wolf movements. Although wolves rarely crossed the BVP during daylight hours in summer, the high frequency of black and grizzly bear road crossings during daylight hours puts bears in jeopardy of being disturbed by humans. This differential response of grizzly and black bears may be more a function of their need to fulfil survival requirements than a lack of response to human use. I documented approaching vehicles interrupting black and grizzly bear crossing attempts of the BVP on a number of occasions, and a progressive change from a wary status to a human-habituated status was seen in the younger adult female grizzly bear as encounters with humans and vehicles along roads increased. At current traffic-volume levels black and grizzly bears are exposed to high human-encounter rates which may eventually result in habituation (Jalkotzy et al. 1999), and a lower probability of survival (Hebblewhite et al. 2003).

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

All three species increased their use of one or more spatial security features (vegetative security cover, road curvature, terrain roughness) at crossing sites used during periods of high traffic volume, indicating a loss of habitat effectiveness and a temporal reduction in permeability of the BVP. This pattern suggests that current traffic levels on the BVP are adversely impacting habitat effectiveness for wolves, black bears and grizzly bears.

Seasonal or permanent road closures have been widely recommended as a management action to benefit wildlife (Lyon 1979; Thurber et al. 1994; Mace et al. 1996; Mace et al. 1999; Gibeau 2000; Forman 2000; Trombulak and Frissell 2000), and a number of studies have documented an increase in road permeability to carnivores when closed to traffic (Brody and Pelton 1989; Kasworm and Manley 1990; Thurber et al.1994). My results indicate that temporal closures of secondary roads, such as the BVP, will assist in restoring habitat effectiveness and connectivity for wolves, black bears and grizzly bears in the Bow River Valley. Elsewhere, programs to improve habitat effectiveness and connectivity for wolves, black bears and grizzly bears must consider the negative effects of traffic volume on these species, and the need to allow bears and wolves to move across the landscape during daylight hours.

Due to the paucity of data, I was unable to develop a suitable model for large carnivore TCH crossings, however amalgamation of data from this and other projects in BNP may result in a large enough sample size to reliably predict large carnivore crossing sites for planning wildlife crossing structures. During three years of study, I detected only one crossing of the unfenced section of the TCH by a grizzly bear, five crossings by wolves, and nine crossings by non-habituated black bears. Only two female black bears crossed this section of the TCH and both were killed during the study period on two-lane primary highways. Of six male black bears that crossed the TCH, two were killed on the TCH, two were killed by National Park Wardens due to habituation, one disappeared from the study area and one continues to live in the study area.

Many studies have documented the TCH as being a significant source of direct mortality and a barrier to cross-valley wildlife movements in BNP (Paquet et al. 1996; Serrouya 1999; Gibeau 2000; Alexander 2001; Callaghan 2002). The urgency to fence and mitigate the untwinned section of the TCH is extreme.

Based on the results of this work, I offer the following management recommendations:

1. Wolf, black bear and grizzly bear crossing frequency of the BVP was negatively influenced by traffic volume but positively influenced by ambient light, suggesting these species may require daylight for cross-valley travel. To increase habitat effectiveness and road permeability and to prevent further

shifts in road-crossing patterns as human use levels of the Bow Valley increase, I recommend the use of temporal road closures along secondary roads, particularly the BVP. Based on temporal road-crossing data collected during this study, I recommend that the BVP be closed to all forms of human travel between 17:00 and noon to allow bears and wolves to cross roads during daylight, crepuscular and night hours, without risk of disturbance by humans. A closure extending throughout the afternoon would benefit all three species, however the importance of human appreciation of the Bow Valley Parkway to greater conservation efforts is recognised. Finally, I recommend that the spatial extent of the temporal closure extend from Castle Junction to Banff.

2. Due to the lack of compliance with the current voluntary travel restriction, I strongly recommend the travel restriction be made mandatory and that a gate be placed at Castle Junction and at Five-Mile Bridge to restrict access. To ensure that cyclists are not accessing the road, compliance should be monitored via remote camera or periodic vehicle patrols by National Park Wardens. This is essential for maintaining habitat effectiveness and public safety.

3. Any increase in use of the Bow Valley Parkway during summer or winter months may further decrease habitat effectiveness for large carnivores. For this reason, I recommend restricting further development of new or existing

facilities along the Bow Valley Parkway. Any proposal aimed at increasing human use or traffic volume along the Bow Valley Parkway should be rejected to maintain and restore the ecological integrity of the parkway habitat.

LITERATURE CITED

Alexander, S.M. 2001. A spatial analysis of road fragmentation and linkage zones for multi-species in the Canadian Rocky Mountains: A winter ecology study. Ph.D. Dissertation. University of Calgary, Alberta. 352pp.

Amstrup, S.C., and J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. *J. Wildl. Manage*. 40(2): 340-348.

Archibald, W.R., R. Ellis, and A.N. Hamilton. 1987. Responses of grizzly bears to logging truck traffic in the Kimsquit River Valley, British Columbia. *Int. Conf. Bear Res. And Manage.* 7: 251-257.

Ayres, L., L.S. Chow, and D.M. Graber. 1986. Black bear activity patterns and human induced modifications in Sequoia National Park. *Int. Conf. Bear Res. and Manage.* 6: 151-154.

Bashore T.L., W.M. Tzilkowski, and E.D. Bellis. 1985. Analysis of deer-vehicle collision sites in Pennsylvania. *J. Wildl. Manage.* 49(3): 769-774.

Bennett, A.F. 1991. Roads, roadsides and wildlife conservation: a review. Pages 99-118 in Saunders, D.A. and R.J. Hobbes, eds. Nature Conservation 2: the role of corridors. Surrey, Beatty and Sons, New South Wales, Australia.

Beringer, J.J., S.G. Seibert, and M.R. Pelton. 1990. Incidence of road crossing by black bears on Pisgah National Forest, North Carolina. *Int. Conf. Bear Res. and Manage.* 8: 85-92.

Bloch, G. and K. Bloch. 2002. The influence of highway traffic on movement patterns of the Bow Valley wolf pack on the Bow Valley Parkway of Banff National Park. Rept. Prep. For Banff National Park, Parks Canada.

Brandenburg, D.M. 1996. Effects of roads on behavior and survival of black bears in coastal North Carolina. M.Sc. Thesis. Univ. of Tennessee, Knoxville. 130pp.

Brody, A.J. and M.R. Pelton. 1989. Effects of roads on black bear movements in western North Carolina. *Wildl. Soc. Bull.* 17: 5-10.

Burnham, K.P. and D.R. Anderson. 1998. Model Selection and Inference: A Practical Information-theroretic Approach. Springer-Verlag, New York. 353pp.

Callaghan, C.J. 2002. The ecology of gray wolf (*Canis lupus*) habitat use, survival and persistence in the Central Rocky Mountains, Canada. Ph.D. Dissertation. University of Guelph, Ontario. 211pp.

Carroll, C., P.C. Paquet, and R.F. Noss. 2000. Modeling carnivore habitat in the Rocky Mountain region: a literature review and suggested strategy. World Wildlife Fund, Toronto, Ontario. 104pp.

Clevenger, A.P. and N. Waltho. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. *Cons. Biol.* 14: 47-56.

Clevenger, A.P., J. Wierzchowski, B. Chruszcz, and K. Gunson. 2002. GIS generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. *Cons. Biol.* 16: 503-514.

Cornwell, L., C. Pacas and J. Green. 1996. Introduction: Ecological Outlooks for the Banff Bow Valley. Chapter 1 in: Green, J., C. Pacas, L. Cornwell and S. Bayley (eds). Ecological Outlooks Project. A Cumulative Effects Assessment and Futures Outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, ON. 20 pp.

Curatolo, J.A. and S.M. Murphy. 1986. The effects of pipelines, roads, and traffic on the movements of caribou, *Rangifer tarandus*. *Can. Field Nat.* 100(2): 218-224.

Davies, K.F., C. Gascon, and C.R. Margules. 2001. Habitat Fragmentation: Consequences, Management, and Future Research Priorities. In Soulé, M.E. and G. H. Orians (Eds.) Conservation Biology: Research Priorities for the Next Decade. Island Press, Washington. 307 pp.

Dyer, S.J. 1999. Movement and distribution of woodland caribou (*Rangifer tarandus*) in response to industrial development in northeastern Alberta. MSc. Thesis. University of Alberta, Canada.

Forman, R.T.T. 2000. Estimate of the area affected ecologically by the road system in the United States. *Cons. Biol.* 14: 31-35.

Forman, R.T.T., D. Sperling, and F.J. Swanson. 2002. Road Ecology: Science and Solutions. Island Press, 424 pp.

Frair, J.L. 1999. Crossing Paths: gray wolves and highways in the Minnesota Wisconsin border region. MSc. Thesis. University of Wisconsin, Wisconsin.

Gibeau, M.L. and S. Herrero. 1998. Roads, rails and grizzly bears in the Bow River Valley, Alberta. p. 104-108 in: Evink, G.L., Garrett, P., Zeigler, D., and Berry, J. (eds.) Proceedings of the International Conference on Wildlife Ecology and Transportation. FL-ER-69-98, Florida Department of Transportation, Tallahassee, Florida. 263pp.

Gibeau, M.L. 2000. A conservation biology approach to management of grizzly bears in Banff National Park, Alberta. Ph.D Dissertation, University of Calgary, Alberta.

Gilpin, M.E. and M.E. Soulé. 1986. Minimum viable populations: processes of species extinction. Pages 19-34 in: M.E. Soulé, ed. Conservation Biology: the science of scarcity and diversity. Sinauer Associates Inc., Massachusetts.

Griffiths, M. and C.P. Van Schaik. 1993. The impact of human traffic on the abundance and activity periods of Sumatran rain forest wildlife. *Cons. Biol.* 7(3): 623-626.

Hebblewhite, M. 2000. Wolf and elk predator-prey dynamics in Banff National Park. M.Sc. Thesis. University of Montana. 130 pp.

Hebblewhite, M., M. Percy, and R. Serrouya. 2003. Black bear (*Ursus americanus*) survival and demography in the Bow Valley of Banff National Park, Alberta. *Biol. Cons.* 112(3): 415-425.

Herrero, S. 1985. Bear attacks: their causes and avoidance. Nick Lyons Books, Winchester Press, Piscataway, New Jersey. 287pp.

Holland, W.D. and G.M. Coen. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Vol. 1. Summary. Alberta Institute of Pedology Publication M-83-2.

Holroyd, G.L., and Van Tighem, K.J. 1983. Ecological (biophysical) land classification of Banff and Jasper national parks. Volume III. The wildlife inventory. Can.Wildl. Serv., Edmonton. 691 pp.

Horejsi, B.L. 1981. Behavioral response of barren ground caribou to a moving vehicle. *Arctic.* 34(2): 180-185.

Hosmer, D.W., and S. Lemeshow. 1989. Applied Logistic Regression. John Wiley and Sons, New York, New York. 307 pp.

Hubbard, M.W., B.J. Danielson, and R.A. Schmitz. 2000. Factors influencing the location of deer-vehicle accidents in Iowa. *J. Wildl. Manage*. 64(3): 707-713.

Inbar, M. and R.T. Mayer. 1999. Spatio-temporal trends in armadillo diurnal activity and road-kills in central Florida. *Wild. Soc. Bull.* 27(3): 865-872.

Jaeger, J.A.G. and L. Fahrig. 2002. Modeling the effects of road network patterns on population persistence: relative importance of traffic mortality and 'fence effect'. *Proceed. Int. Conf. on Ecol. and Transport*. 2001. p. 298 - 312.

Jalkotzy, M., Ross, P.I., and M.D. Nasserden. 1997. The effects of linear developments on wildlife: a review of selected literature. ARC Wildlife Services Ltd. Calgary, AB. 440 pp. Prepared for the Canadian Association of Petroleum Producers, Alberta Energy and Utilities Board, and Nova Corporation. 224 pp.

Jalkotzy, M.G., R.R. Riddell, and J. Wierzchowski. 1999. Grizzly bears, habitat and humans in the Skoki, Baker, South Pipestone, and Lake Louise bear management units, Banff National Park. Prepared for Parks Canada and the Skiing Louise Group. Arc Wildlife Services Ltd., Riddell Environmental Research Ltd., and Geomar Consulting Ltd. 101pp.

James, A.R.C. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in Northeastern Alberta. MSc. Thesis. University of Alberta, Canada.

Jensen, W.F., Fuller, T.K., and W.L. Robinson. 1986. Wolf, *Canis lupus*, distribution on the Ontario-Michigan border near Sault Ste. Marie. *Can. Field Nat*. v 100: p. 363 - 366.

Kasworm, W. and T. Manley. 1990. Road and trail influences on grizzly bears and black bears in Northwest Montana. *Int. Conf. Bear Res. and Manage*. 8: 79-84.

Lariviere, S., J. Huot, and C. Samson. 1994. Daily activity patterns of female black bears in a northern mixed-forest environment. *J. Mamm*. 75(3):613 620.

Lovallo, M.J., and E.M. Anderson. 1996. Bobcat movements and home ranges relativeto roads in Wisconsin. *Wildl. Soc. Bull*. 24(1): 71-76.

Lyon, L.J. 1979. Habitat effectiveness for elk as influenced by roads and cover. *J. For*. 1979. 658-660.

Mace, R.D., J.S. Waller, T.L. Manley, L.J. Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. *J. Appl. Ecol.* 33: 1395-1404.

Mace, R.D., J.S. Waller, T.L. Manley, K. Ake, and W.T. Wittinger. 1999. Landscape evaluation of grizzly bear habitat effectiveness in Western Montana. *Cons. Biol.* 3: 367-377.

Mader, H.J. 1984. Animal habitat isolation by roads and agricultural fields. *Biol. Cons*. 29: 81-96.

Manly, B.F.J., L. McDonald, and D. Thomas. 1993. Resource selection by animals: Statistical design and analysis. Chapman and Hall, New York.

Mattson D.J., Knight, R.R., and B.M. Blanchard. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. *Int. Conf. Bear Res. and Manage*. 7:259-273.

McLellan, B.N., and D.M. Shackleton. 1988. Grizzly bears and resource extraction industries: effects of roads on behaviour, habitat use and demography. *J. Appl. Ecol.* 25: 451-460.

Mech, L.D., Fritts, S.H., Radde, G.L., and W.J.Paul. 1988. Wolf distribution and road density in Minnesota. *Wildl. Soc. Bull*. v. 16: p. 85-87.

Mech, L.D. 1970. The wolf: the ecology and behavior of an endangered species. University of Minnesota Press, Minneapolis, MN. 394 pp.

Menard, S. 1995. Applied Logistic Regression Analysis. Sage Publications Inc., London. Series No. 07-106. 97pp.

Murphy, S.M., and J.A. Curatolo. 1987. Activity budgets and movement rates of caribou encountering pipelines, roads, and traffic in northern Alaska. *Can. J. Zool.* 65: 2483-2490.

Noss, R.F., H. Quigley, M. Hornhocker, T. Merrill, and P. Paquet. 1996. Conservation biology and carnivores: conservation in the Rocky Mountains. *Cons. Biol.* 10: 949-963.

Pacas, C. 1996. Human use in the Banff Bow Valley: Past, present and future. Chapter 3 in: Green, J., C. Pacas, L. Cornwell and S. Bayley (eds.). Ecological Outlooks Project. A Cumulative Effects Assessment and Futures Outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, ON. 77pp.

Paquet, P.C. 1993. Summary reference document – ecological studies of recolonizing wolves in the Central Canadian Rocky Mountains. Unpubl. Rep. By John/Paul and Assoc. for Canadian Parks Service, Banff, AB. 176 pp.

Paquet, P.C., J. Wierzchowski, and C. Callaghan. 1996. Effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 in: Green, J., C. Pacas, L. Cornwell and S. Bayley (eds.). A Cumulative Effects Assessment and Futures Outlook for the Banff Bow Valley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, ON. 74 pp.

Percy, M.P., T. Hurd, and C. Callaghan. 1998. Spatial and temporal effects of the Bow Valley parkway on wolf movement and habitat use. Unpublished Report Prepared for Parks Canada, Banff Alberta. 33 pp.

Percy, M.P. 1999. Summary of black bear trapping, Road Effects on Large Carnivores Project. May - June 1999. Unpublished Report Prepared for Parks Canada, Banff Alberta. 25p.

Philcox, C.K., A.L. Grogan, and D.W. MacDonald. 1999. Patterns of otter *Lutra lutra* road mortality in Britain. *J. Appl. Ecol.* 36: 748-762.

Rost, G.R. and J.A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. *J. Wildl. Manage.* 43(3): 634-641.

Saunders, D.A., Hobbs, R.J., and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Cons. Biol.* 5(1): 18-32.

Serrouya, R. 1999. Permeability of the Trans Canada Highway to black bear movements in the Bow Valley of Banff National Park. MSc. Thesis University of British Columbia.

Servheen, C., J. Waller, and W. Kasworm. 1998. Fragmentation effects of high speed highways on grizzly bear populations shared between the United States and Canada. p. 97-103 in: Evink, G.L., D. Zeigler, and J. Berry, eds. Proceedings of the International Conference on Wildlife Ecology and Transportation. FL-ER-69-98, Florida Department of Transportation, Tallahassee, Florida. 263pp.

Stevens, S., C. Mamo, T. Shury, and M.L. Gibeau. 1999. Eastern slopes grizzly bear project capture program. Unpublished report for the Eastern Slopes Grizzly Bear Project Steering Committee, University of Calgary.

Sokal, R.R., and F.J. Rohlf. 1995. Biometry. W.H. Freeman and Company, New York. 887 pp.

Tabachnik, B.G. and L.S. Fidell. 2001. Using Multivariate Statistics. Fourth Edition. Allyn and Bacon, Massachusetts. 966pp.

Thiel, R.P. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. *Amer. Midl. Nat.* v 113(2): p. 404-407.

Thurber, J.M., R.O. Peterson, T.D. Drummer, and S.A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wild. Soc. Bull.* 22: 61-68.

Trombulak, S.C. and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Cons. Biol.* 14: 18-30.

Weaver, J., P. Paquet, and L. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Cons. Biol.* 10: 964-976.

White, G.C. and R.A. Garrott. 1990. Analysis of Wildlife Radio Tracking Data. Academic Press Inc. 383 pp.

Whittington, J. 2002. Movement of wolves (*Canis lupus*) in response to human development in Jasper National Park, Alberta. MSc. Thesis. University of Alberta, Canada. 86 pp.

Wilcox, B.A. and D.D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *Am. Nat.*, 125: 879-887.

Zar, J.H. 1999. Biostatistical Analysis. Fourth Edition. Prentice-Hall Inc. New Jersey. 663 pp.

Table 2-1: Summary of road crossings by radio-collared wolves, black bears and grizzly bears in the Bow Valley of Banff National Park, May 1998 to March 2001. (Number of crossings of each road type detected during 24-hour monitoring is included in parentheses).

	Number of Crossings		
	Wolf	**Black bear**	**Grizzly bear**
BVP	118 (114)	115 (104)	29 (25)
Other Secondary Rds	48 (46)	20 (15)	6 (5)
TCH (unfenced)	5 (5)	30 (22)	1 (1)
TCH (fenced)	49 (49)	7 (7)	1 (0)
Hwy 93 North	1 (1)	3 (1)	0
Hwy 93 South	3 (3)	5 (5)	0
Totals	224 (218)	180 (154)	37 (31)

Table 2-2: Spearmans Correlation Matrix of Spatial and Temporal Road-Crossing Variables (Abbreviations are: DW = Drainage Distance; DLUL = Distance to Low/Non-use Linear Feature; R = Terrain Roughness; S = Vegetative Security Cover; C = Road Curvature; DH = Distance to area of High Human Use; TV = Traffic Volume; L = Light)

Variable	DW	DLUL	R	S	C	DH	TV	L
DW	1.000							
DLUL	0.006	1.000						
R	0.006	0.109	1.000					
S	0.297	0.024	-0.052	1.000				
C	-0.115	-0.214	0.448	0.061	1.000			
DH	-0.031	0.039	0.318	0.051	0.241	1.000		
TV	-0.068	0.110	-0.050	-0.117	-0.084	0.034	1.000	
L	-0.065	0.006	0.052	0.021	0.038	0.084	0.705	1.000

Table 2-3: Results of Mann-Whitney U tests comparing use of BVP road-crossing variables by habituated versus non-habituated black bears. (Variable abbreviations defined in Table 2-2).

Road Crossing Variable	P Value	U Statistic
C	P = 0.09	1254.0
S	P = 0.39	1386.0
DH	P = 0.34	1368.5
R	P = 0.53	1426.0
DLUL	P = 0.58	1627.5
DW	P = 0.44	1401.5
L	P = 0.79	1506.5
TV	P = 0.47	1409.5

Table 2-4: Results of matched-case control logistic regression examining differences between actual and estimated spatial road-crossing attributes. (Variable abbreviations defined in Table 2-2).

Parameter	Estimate	Standard Error	t-ratio	P-value
S	0.03953	0.03592	1.10038	0.27117
R	0.69685	0.72893	0.95599	0.33908
DLUL	0.00223	0.00220	1.01220	0.31144
DW	-0.00087	0.00316	-0.27522	0.78315
DH	-0.00130	0.00113	-1.15002	0.25013
C	-0.07753	0.06247	-1.24115	0.21455

Table 2-5: Top set of wolf models for BVP crossing events. (Variable abbreviations defined in Table 2-2).

Model #	Model Terms	K	LL	AIC_c	ΔAIC_c	w_i
40	R,DH,L,TV,S*TV,C*TV,DH*L	9	-169.355	357.331	0.000	0.1775
36	S,DH,DLUL,L,TV,DH*L,S*TV	9	-169.829	358.279	0.948	0.1105
32	S,DH,L,TV,DH*L,S*TV,C*TV	9	-169.970	358.561	1.230	0.0960
22	DH,DLUL,L,TV,TV*C,TV*S,L*DH	9	-170.004	358.628	1.297	0.0928
37	S,DH,DLUL,L,TV,R,DH*L,S*TV	10	-168.945	358.651	1.320	0.0918
23	DH,L,TV,TV*C,TV*S,DH*L	8	-171.317	359.129	1.798	0.0723
26	DH,L,TV,TV*S,DH*L	7	-172.631	359.645	2.314	0.0558
21	DH,DLUL,L,TV,TV*S,DH*L	8	-171.643	359.781	2.449	0.0522
33	S,DH,L,TV,DH*L,C*TV	8	-171.691	359.876	2.545	0.0497
43	S,R,L,TV,TV*S,DH*L	8	-171.876	360.248	2.916	0.0413
41	DLUL,L,TV,TV*S,TV*C,DH*L	8	-172.346	361.187	3.856	0.0258
42	S,R,L,TV,TV*S,TV*C	8	-172.365	361.225	3.894	0.0253

Table 2-6: Averaged beta coefficients, standard errors and relative importance of variables in averaged BVP wolf crossing model. (Variable abbreviations defined in Table 2-2).

Variable	Parameter Estimate	Standard Error	Upper 90% CI	Lower 90% CI	t-value	Rank
Intercept	-1.41236	0.68957	-0.27458	-2.55015	1.650	
L	0.87565	0.27620	1.33138	0.41991	1.650	1
TV	-0.08878	0.04011	-0.02259	-0.15496	1.650	2
DH*L	-0.00027	0.00011	-0.00008	-0.00046	1.650	3
DH	0.00028	0.00014	0.00051	0.00005	1.650	4
TV*S	0.00100	0.00050	0.00182	0.00017	1.650	5
TV*C	0.00191	0.00115	0.00381	0.00001	1.650	6
DLUL	-0.00068	0.00046	0.00008	-0.00144	1.650	7
R	-0.21811	0.14134	0.01511	-0.45132	1.650	8
S	0.01530	0.00919	0.03045	0.00014	1.650	9

Table 2-7: Prediction Success Table for averaged wolf road crossing model.

	Crossing	No Crossing
Crossing	42.776	57.224
No Crossing	57.224	142.776
Total	100	200
Correct	0.428	0.714
Total Correct	0.619	

Table 2-8: Top set of black bear models for BVP crossing events. (Variable abbreviations defined in Table 2-2).

Model #	Model Terms	K	LL	AIC_c	ΔAIC_c	w_i
6	DH,L	4	-172.664	353.464	0.000	0.2514
2	DH,R,L	5	-172.181	354.566	1.102	0.1449
11	DH,L,TV	5	-172.320	354.845	1.380	0.1261
3	DH,R,L,TV	6	-171.678	355.643	2.178	0.0846
9	DH,R,L,TV*L	6	-171.748	355.783	2.318	0.0789
12	DH,R,L,TV,TV*C,TV*R	8	-169.865	356.225	2.760	0.0632
7	DH,R,L,TV*C	6	-172.010	356.307	2.842	0.0607
13	DH,R,L,TV*C,TV*R,TV*L	8	-169.923	356.341	2.877	0.0597

Table 2-9: Averaged beta coefficients, standard errors and relative importance of variables in averaged BVP black bear crossing model. (Variable abbreviations defined in Table 2-2).

Variable	Parameter Estimate	Standard Error	Upper 90% CI	Lower 90% CI	t-value	Rank
Intercept	-2.64358	0.43970	-1.91807	-3.36909	1.650	
L	0.92821	0.22610	1.30127	0.55514	1.650	1
DH	0.00022	0.00010	0.00039	0.00006	1.650	2
R	-0.17206	0.17090	0.10993	-0.45405	1.650	3
TV*R	0.00236	0.00171	0.00519	-0.00046	1.650	4
TV	0.00206	0.00249	0.00616	-0.00204	1.650	5
TV*L	0.00099	0.00132	0.00316	-0.00119	1.650	6
TV*C	-0.00031	0.00031	0.00020	-0.00083	1.650	7

Table 2-10: Prediction Success Table for averaged black bear road crossing model.

	Crossing	No Crossing
Crossing	41.959	58.041
No Crossing	58.041	141.959
Total	100	200
Correct	0.420	0.710
Total Correct	0.613	

Table 2-11: Top set of grizzly bear models for BVP crossing events. (Variable abbreviations defined in Table 2-2).

Model #	Model Terms	K	LL	AIC_c	ΔAIC_c	w_i
25	C,S,DLUL,TV*C,TV*S,L*DH,TV*R	9	-35.437	91.560	0.000	0.1378
43	TV*C,TV*S,TV*R,DH*L	6	-39.340	91.879	0.319	0.1175
3	C,S,DLUL,TV*C,L*S,TV*S,L*DH,TV*R	10	-34.636	92.605	1.046	0.0817
34	S,DLUL,TV*C,TV*S,TV*R,DH*L,L*S	9	-36.088	92.864	1.304	0.0718
32	S,DLUL,TV*S,DH*L,TV*R	7	-38.683	92.990	1.430	0.0674
44	TV*C,S*TV,DH*L	5	-41.077	92.998	1.438	0.0671
23	C,DLUL,TV*R,TV*C,L*DH	7	-38.709	93.041	1.481	0.0657
41	DLUL,TV*C,TV*S,TV*R,DH*L,L*S	8	-37.561	93.239	1.679	0.0595
39	DLUL,TV*S,TV*R,DH*L	6	-40.160	93.520	1.960	0.0517
42	TV*C,S*TV,DH*L,TV*R,L*S	7	-39.056	93.735	2.175	0.0464
22	C,S,TV*C,TV*S,TV*R,DH*L	8	-37.813	93.744	2.184	0.0462
33	S,DLUL,TV*S,DH*L,TV*R,L*S	8	-38.100	94.317	2.757	0.0347
37	DLUL,TV*C,DH*L	5	-42.029	94.902	3.343	0.0259
18	C,S,TV*R,L*DH	6	-40.992	95.185	3.625	0.0225

Table 2-12: Averaged beta coefficients, standard errors and relative importance of variables in averaged BVP grizzly bear crossing model. (Variable abbreviations defined in Table 2-2).

Variable	Parameter Estimate	Standard Error	Upper 90% CI	Lower 90% CI	t-value	Rank
Intercept	-2.95407	1.59671	-0.29556	-5.61259	1.665	
DH*L	0.00032	0.00012	0.00051	0.00012	1.665	1
TV*R	0.00401	0.00211	0.00751	0.00050	1.665	2
TV*C	-0.00213	0.00128	0.00000	-0.00426	1.665	3
DLUL	-0.00234	0.00129	-0.00019	-0.00449	1.665	4
S	0.03657	0.02655	0.08079	-0.00764	1.665	5
TV*S	0.00013	0.00012	0.00034	-0.00007	1.665	6
C	0.18857	0.14309	0.42682	-0.04969	1.665	7
L*S	-0.00955	0.00970	0.00817	-0.00820	1.665	8

Table 2-13: Prediction Success Table for averaged grizzly bear road crossing model.

	Crossing	No Crossing
Crossing	13.845	11.155
No Crossing	11.155	40.845
Total	25	52
Correct	0.554	0.786
Total Correct	71.03	

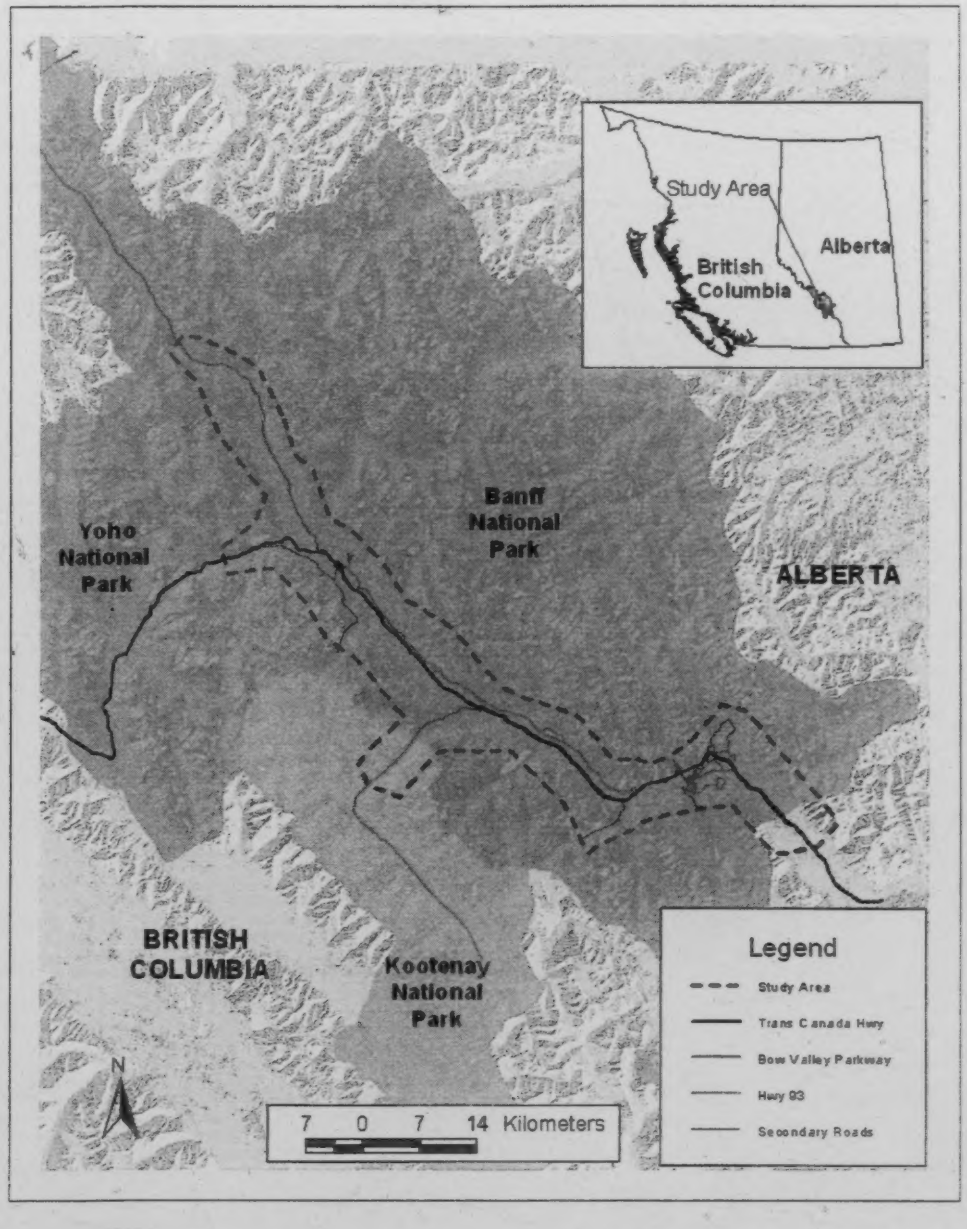

Figure 2-1: The greater Banff National Park region illustrating the study area.

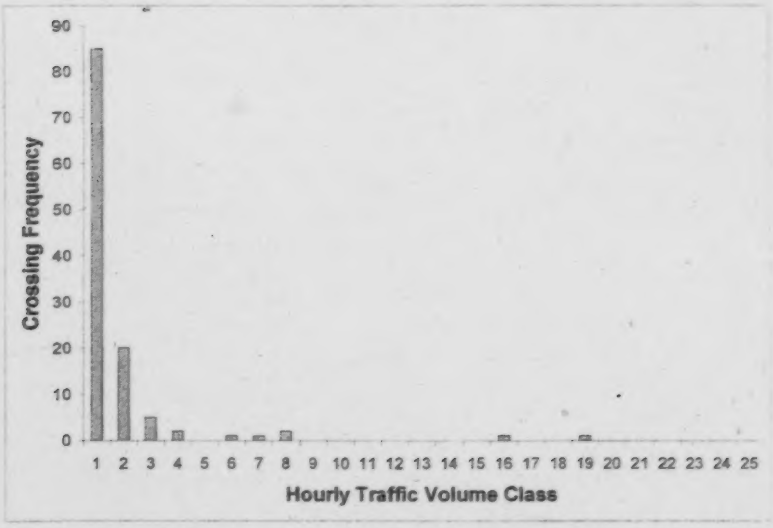

Figure 2-2: Wolf crossing frequency of the Bow Valley Parkway relative to hourly traffic volume class (Class Interval = 10 vehicles per hour). May 1998 through March 2001.

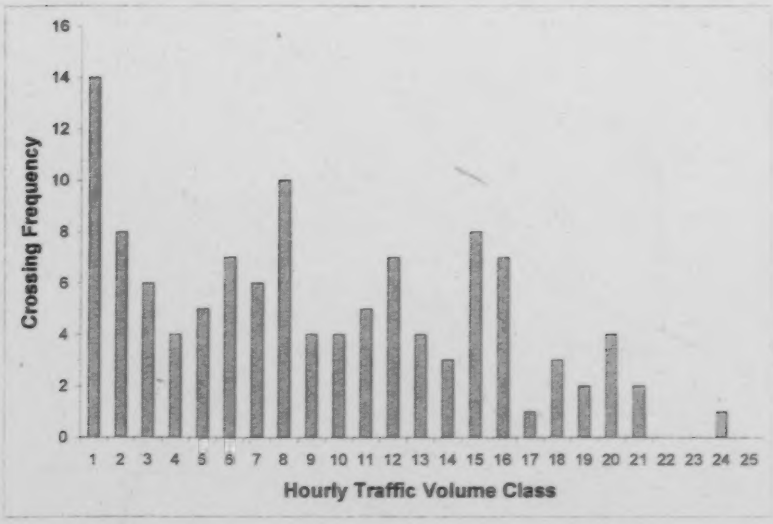

Figure 2-3: Black bear crossing frequency of the Bow Valley Parkway relative to hourly traffic volume class (Class Interval = 10 vehicles per hour). May 1998 through November 2000.

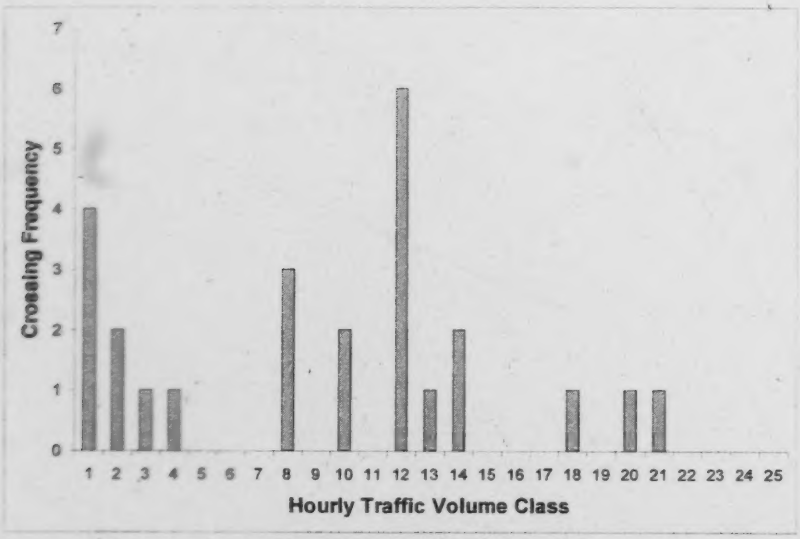

Figure 2-4: Grizzly bear crossing frequency of the Bow Valley Parkway relative to hourly traffic volume class (Class Interval = 10 vehicles per hour). May 1998 through September 2000.

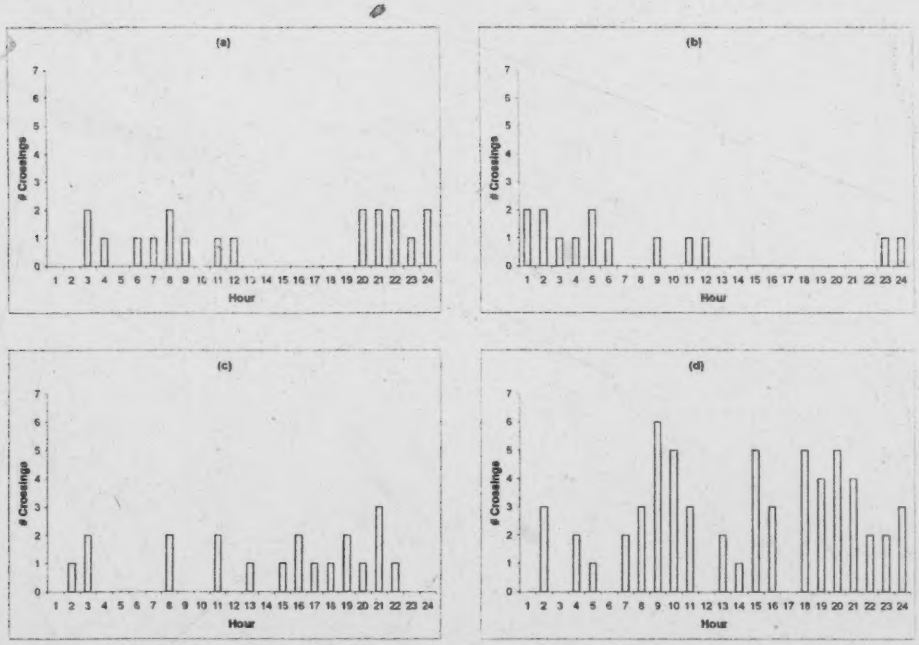

Figure 2-5: Hourly frequency of Bow Valley Parkway crossings by wolves in Banff National Park during (a) spring (n = 19), (b) summer (n = 14), (c) fall (n = 20), and (d) winter (n = 61). 1998 to 2001.

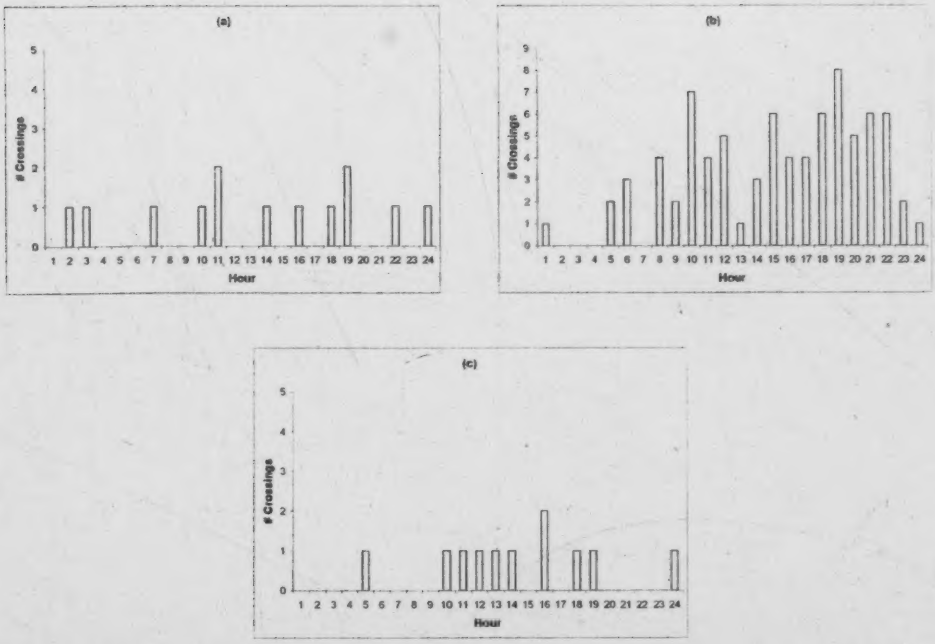

Figure 2-6: Hourly frequency of Bow Valley Parkway crossings by black bears in Banff National Park during (a) spring (n = 13), (b) summer (n = 80); and (c) fall (n = 11). 1998 to 2001.

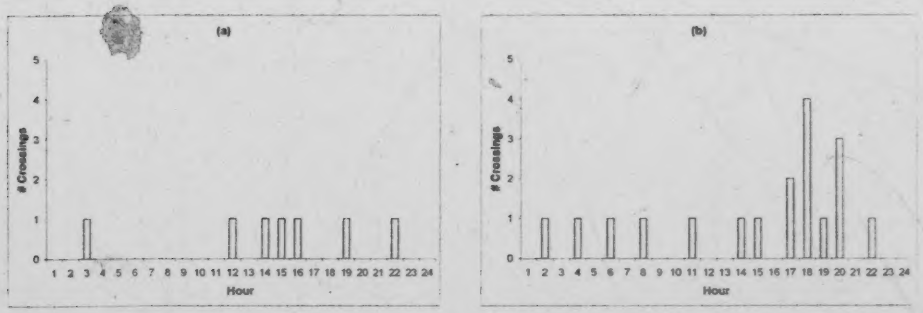

Figure 2-7: Hourly frequency of Bow Valley Parkway crossings by grizzly bears in Banff National Park during (a) spring (n = 7) and (b) summer (n = 18). 1998 to 2001.

APPENDIX 1

Set of candidate models for determining spatial and temporal variables important to wolf crossing events of the BVP. A total of 44 models were included in the candidate set. Variable abbreviations are as follows: DLUL = Distance to Low/Non-use Linear Feature; R = Terrain Roughness; S = Vegetative Security Cover; C = Road Curvature; DH = Distance to area of High Human Use; TV = Traffic Volume; L = Light.

Model #	Model Terms
1.	Global Model - all terms
2.	Intercept-only Model
3.	S+R+DH+DLUL
4.	S+R+DH+L
5.	S+R+DH+TV
6.	S+R+DH+TV*S
7.	S+R+DH+TV*C
8.	S+R+DH+DH*L
9.	DH+DLUL+L+TV
10.	DH+DLUL+L+TV*S
11.	DH+DLUL+L+TV*C
12.	DH+DLUL+L+DH*L
13.	DH+DLUL+TV+TV*S
14.	DH+DLUL+TV+TV*C
15.	DH+DLUL+TV+DH*L
16.	DH+DLUL+L+TV+TV*C
17.	DH+DLUL+L+TV+TV*S
18.	DH+DLUL+L+TV+DH*L
19.	DH+DLUL+L+TV+TV*C+TV*S
20.	DH+DLUL+L+TV+TV*C+DH*L
21.	DH+DLUL+L+TV+TV*S+DH*L
22.	DH+DLUL+L+TV+TV*C+TV*S+DH*L
23.	DH+L+TV+TV*C+TV*S+DH*L
24.	DH+L+TV+TV*C+TV*S
25.	DH+L+TV+TV*C+DH*L
26.	DH+L+TV+TV*S+DH*L
27.	DH+L+TV+TV*S
28.	DH+L+TV+DH*L
29.	S+R+DH+L+TV
30.	S+R+DH+DLUL+L+TV
31.	S+DH+DLUL+L+TV+TV*S
32.	S+DH+L+TV+TV*S+TV*C+DH*L

Appendix 1 cont.

Model #	Model Terms
33.	S+DH+L+TV+TV*C+DH*L
34.	S+R+DH+DLUL+TV*S
35.	S+DLUL+L+TV+DH*L
36.	S+DH+DLUL+L+TV+DH*L+TV*S
37.	S+DH+DLUL+L+TV+R+DH*L+TV*S
38.	R+DH+DLUL+L+TV+TV*S
39.	R+DH+L+TV+TV*S+TV*C
40.	R+DH+L+TV+TV*S+TV*C+DH*L
41.	DLUL+L+TV+TV*S+TV*C+DH*L
42.	S+R+L+TV+TV*S+TV*C
43.	S+R+L+TV+TV*S+DH*L
44.	S+R+L+TV+DH*L+TV*C

APPENDIX 2

Set of candidate models for determining spatial and temporal variables important to black bear crossing events of the BVP. A total of 26 models were included in the candidate set. Variable abbreviations are as follows; R = Terrain Roughness; C = Road Curvature; DH = Distance to area of High Human Use; TV = Traffic Volume; L = Light.

Model #	Model Terms
1.	DH+R
2.	DH+R+L
3.	DH+R+L+TV
4.	R+L+TV
5.	DH+R
6.	DH+L
7.	DH+R+L+TV*C
8.	DH+R+TV*R
9.	DH+R+L+TV*L
10.	R+L
11.	DH+L+TV
12.	DH+R+L+TV+TV*C+TV*R
13.	DH+R+L+TV*C+TV*R+TV*L
14.	R+L+TV+TV*C

Appendix 2 cont.

Model #	Model Terms
15.	R+L+TV*R+TV*L
16.	TV+TV*R+TV*L+TV*C
17.	R+TV
18.	R+DH+TV
19.	DH+TV*R+TV*C+TV*L
20.	DH+TV
21.	L+TV
22.	DH+TV*C
23.	DH+R+L+TV*L
24.	TV*C+TV*L+TV*R
25.	Global Model - all terms
26.	Intercept-only Model

APPENDIX 3

Set of candidate models for determining spatial and temporal variables important to grizzly bear crossing events of the BVP. A total of 44 models were included in the candidate set. Variable abbreviations are as follows: DLUL = Distance to Low/Non-use Linear Feature; R = Terrain Roughness; S = Vegetative Security Cover; C = Road Curvature; DH = Distance to area of High Human Use; TV = Traffic Volume; L = Light.

Model #	Model Terms
1.	Global Model - all terms
2.	Intercept-only Model
3.	C+S+DLUL+TV*C+L*S+TV*S+DH*L+TV*R
4.	C+S+DLUL+TV*C
5.	C+S+DLUL+L*S
6.	C+S+DLUL+TV*S
7.	C+S+DLUL+DH*L
8.	C+S+DLUL+TV*R
9.	C+S+TV*C+L*S
10.	C+S+TV*C+TV*S
11.	C+S+TV*C+DH*L
12.	C+S+TV*C+TV*R
13.	C+S+L*S+TV*S
14.	C+S+L*S+DH*L
15.	C+S+L*S+TV*R

Appendix 3 cont.

Model #	Model Terms
16.	C+S+TV*S+DH*L
17.	C+S+TV*S+TV*R
18.	C+S+TV*R+DH*L
19.	C+DLUL+TV*C+TV*S+L*S
20.	C+DLUL+TV*S+DH*L+TV*R
21.	C+S+TV*C+TV*S+TV*R+L*S
22.	C+S+TV*C+TV*S+TV*R+DH*L
23.	C+DLUL+TV*R+TV*C+DH*L
24.	C+S+DLUL+TV*C+TV*S+DH*L
25.	C+S+DLUL+TV*C+TV*S+DH*L+TV*R
26.	S+DLUL+TV*C+TV*S
27.	S+DLUL+TV*C+DH*L
28.	S+DLUL+TV*C+L*S
29.	S+DLUL+TV*C+TV*R
30.	S+DLUL+TV*C+TV*S+DH*L
31.	S+DLUL+TV*S+DH*L+L*S
32.	S+DLUL+TV*S+DH*L+TV*R
33.	S+DLUL+TV*S+DH*L+TV*R+L*S
34.	S+DLUL+TV*C+TV*S+TV*R+DH*L+L*S
35.	DLUL+TV*C+TV*S
36.	DLUL+TV*C+TV*R
37.	DLUL+TV*C+DH*L
38.	DLUL+TV*C+L*S
39.	DLUL+TV*S+TV*R+DH*L
40.	DLUL+TV*S+TV*R+DH*L+L*S
41.	DLUL+TV*C+TV*S+TV*R+DH*L+L*S
42.	TV*C+TV*S+TV*R+DH*L+L*S
43.	TV*C+TV*S+TV*R+DH*L
44.	TV*C+TV*S+DH*L

CHAPTER 3

TEMPORAL MOVEMENT PATTERNS OF WOLVES, BLACK BEARS AND GRIZZLY BEARS IN THE BOW VALLEY OF BANFF NATIONAL PARK

INTRODUCTION

Wildlife movement and activity patterns are the result of a complex balance of the need to satisfy biological objectives such as nutrition and reproduction, while minimizing the costs and risks associated with a specific environment (Daan 1981; Alkon and Saltz 1988). A number of variables may influence wildlife movement and activity patterns including ambient light (Alkon and Saltz 1988; Drew and Bissonette 1997), weather (Garshelis and Pelton 1980; Strang 1983), habitat cover (Garshelis et al. 1983; Clevenger et al. 1990), risk of predation (Alkon and Saltz 1988; Lariviere and Messier 1997), prey activity patterns (Clevenger 1993; Lariviere and Messier 1997), food production and type (Garshelis and Pelton 1980; Brandenburg 1996), season (Garshelis et al. 1983; Brandenburg 1996), and human disturbance (Andelt and Gipson 1979; Garshelis and Pelton 1980; Roth 1983; Roth and Huber 1986; Bjarvall and Sandegren 1987; Alkon and Saltz 1988; Clevenger et al. 1990; Clevenger 1993).

Roth (1983) suggested that activity patterns may indicate stresses to a population, and that animals are capable of modifying their activity according to their

environment. Once baseline activity patterns are determined, they can be used to gauge the impacts of ecosystem change on wildlife. This is particularly important in high human-use areas, to identify the potential impacts of human activity on wildlife movement through space and time. Naturally diurnal species may shift to nocturnal movement patterns to avoid encounters with humans, and wary species may be displaced from high quality habitat during peak periods of human activity (Griffiths and Van Schaik 1993). Temporal alienation of habitat resulting from human-induced pressure may precede spatial alienation and the ultimate abandonment of habitat (Paquet et al. 1996). Knowledge of wildlife movement patterns can be applied to temporal human-use management initiatives to increase or maintain habitat effectiveness and landscape connectivity for sensitive species.

The objectives of this study were (*1*) to test whether the movement patterns of wolves (*Canis lupus*), black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos*) change throughout the 24-hour day and between seasons in a heavily fragmented, high human-use landscape, (*2*) to test whether wolf movement patterns during denning/rendezvous season are influenced by the presence of pups, (*3*) to test whether differences exist in daily movement patterns of wary versus human-habituated black bears, and (*4*) to determine how wolves, black bears, and grizzly bears use wildlife corridors and areas of high human-use through time relative to the surrounding landscape.

Wildlife corridors are linear two-dimensional landscape elements that can provide animals with secure movement opportunities by connecting disjunct habitat patches within fragmented landscapes (Gilpin and Soulé 1991). Eleven locally and regionally significant wildlife corridors exist within the Banff Bow Valley ranging in size from 2 km^2 to 26 km^2 (Duke 2000). As human-use levels continue to rise in BNP, maintenance of habitat effectiveness within wildlife corridors is critical to preserve their ability to serve as linkage zones for wildlife movement. Changes in spatial and temporal wildlife movement patterns through wildlife corridors may indicate changes in permeability to more sensitive species such as wolves and grizzly bears.

Previous studies addressing activity patterns of wolves, grizzly bears and black bears suggest that while natural variables influence daily and seasonal activity patterns, such patterns may ultimately be dictated by human activity in areas of high human disturbance (Roth and Huber 1986; Van Dyke et al. 1986; Bjarvall and Sandegren 1987; Clevenger et al. 1990;Vila et al. 1995).

I used biological rather than human-use seasons to describe movement patterns, as the influences of biological season may be more important to overall wolf and bear movement patterns in the Bow Valley. The wolf denning/rendezvous season and the black and grizzly bear spring and berry seasons correspond to the high tourist season in BNP, allowing inferences to be made regarding the possible effect of human activity on wolf and bear movement patterns.

I hypothesised that wolves, wary black bears and grizzly bears would be most active when human activity was lowest, with little movement during daylight hours when human use of the valley is high (i.e. late spring and summer months). I predicted that wary black bears would be more crepuscular and nocturnal than human-habituated black bears. I expected wolves, grizzly bears and wary black bears to use wildlife corridors and areas of high human-use primarily at night and during dawn and dusk, and that human-habituated black bears would show no temporal pattern in their use of these areas. Finally, wolf denning activity may result in distinct temporal movement patterns during spring and summer as wolves may remain at the den site during daylight hours to guard young pups against diurnal predators such as black and grizzly bears. The production of pups in one year of this study followed by the absence of pups in a subsequent year, allowed inferences to be made regarding the influence of denning activity on temporal wolf movement patterns.

STUDY AREA

The study was conducted from May 1998 to March 2001 in the Bow River Valley of Banff National Park, located between 120 and 200 kilometres west of the city of Calgary, Alberta, in the Front and Main ranges of the Canadian Rocky Mountains (Figure 3-1). The park is approximately 6640 km^2 in area and is characterised by rugged mountainous topography. The Bow Valley ranges from approximately two to six kilometres in width, is oriented on a NW to SE axis,

with valley-bottom elevations ranging from approximately 1330 to 2000 metres. Steep mountains and ridges create natural fragmentation of the landscape, while infrastructure required to accommodate more than five million visitors per year (Cornwell et al. 1996) has subjected the landscape to extensive human-induced fragmentation.

Habitat within the study area is classified as belonging to the montane, subalpine or alpine ecoregion (Holland and Coen 1983) depending on elevation. Vegetation is dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), Engelmann spruce (*Picea Engelmannii*), subalpine fir (*Abies lasiocarpa*), poplar (*Populus sp.*) and Douglas fir (*Pseudotsuga menziesii*) forests, grassy slopes, shrubby wetland complexes, and alpine meadows. In addition to wolves, black bears and grizzly bears, large terrestrial fauna found within the study area include elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemonius*), bighorn sheep (*Ovis canadensis*), mountain goat (*Oreamnos americanus*), moose (*Alces alces*), wolverine (*Gulo gulo*), cougar (*Puma concolor*), lynx (*Felis lynx*) and coyote (*Canis latrans*). Climate is characterised by long, cold winters, and relatively short, dry summers.

Four major transportation corridors lie within the study area: the Trans Canada Highway, the Canadian Pacific Railway, Highway 93, and the Bow Valley Parkway. The town of Banff (approximately 6500 permanent residents), the village of Lake Louise (approximately 1500 residents), ten drive-in campgrounds,

numerous outlying commercial resorts/hotels and high day-use areas (picnic grounds, etc.) occur within the study area.

METHODS

Field Methods

Data were collected from two wolves (the alpha male of the Bow Valley Pack [M1], and an adult male of the Fairholme Pack [M2]), eighteen black bears (11 male (9 adult, 2 subadult); 7 female (6 adult; 1 subadult)) and three grizzly bears (1 adult male; 2 adult female) equipped with conventional VHF radio collars (Lotek Engineering, Newmarket, Ontario). Wolves were captured in modified steel foot-hold traps (toothed and padded No. 4 offset foot-hold traps, Livestock Protection Co., Alpine, TX), immobilised with a tiletamine hydrochloride/zolazepam hydrochloride mixture (Telazol™ at 5 mg/kg), and fitted with VHF radio-collars (see Hebblewhite 2000). Black and grizzly bears were captured in steel culvert traps, mesh guillotine traps, or in Aldrich foot snares using natural bait, immobilised with Telazol™ (4-6 mg/kg for black bears, 7-9 mg/kg for grizzly bears), or with a Telazol™/Xylazine (Rompun™) mixture (2mg/kg:1mg/kg for black bears, 3 mg/kg:1mg/kg for grizzly bears) administered intramuscularly via jab stick or projectile dart. Ketamine hydrochloride (Ketaset™, 2mg/kg) was used to lengthen or deepen anaesthesia, if necessary.

I monitored animals from accessible roads in the study area between May 1998 and March 2001. Wolves were monitored on a year-round basis, and black and grizzly bears were monitored from den emergence (early April to mid-May) to den entry (mid-October to mid-November) of each year. Animal location was determined using conventional radio-triangulation techniques (White and Garrott 1990). Telemetry bearings were plotted on 1:20,000 geo-corrected air photos with the use of a hand-held global positioning system (GPS) unit (Garmin 12XL, Garmin International Inc.), and the animals' locations were recorded in UTM co-ordinates. Care was taken to avoid conducting telemetry in such proximity to animals that I risked disturbing them and influencing their movements.

Approximately three times per week, I conducted continuous 24-hour radio-telemetry monitoring sessions, focusing on one to three animals per session. I obtained one wolf location every hour, and one grizzly bear or black bear location every two hours for 24 consecutive hours. Wolves were relocated more frequently as they typically travel faster than bears. Telemetry error was assessed using stationary test collars placed at various locations throughout the study area between 300 and 1500 metres from roads. Conventional triangulation was used to assess average error, which was approximately ±150 metres, consistent with other telemetry-based research in Banff National Park (Serrouya 1999, Gibeau 2000, Hebblewhite 2000, Callaghan 2002).

GIS, Spatial and Temporal Data

Animal locations were converted to spatial GIS (Geographic Information System) files using Arcview 3.2 (ESRI Inc., Redlands, CA.). Hourly movement distances were calculated as the straight-line distance between consecutive hourly telemetry locations, or the straight-line distance between consecutive bihourly locations divided by two. Minimum daily movement distances were calculated as the sum of all straight-line distances between the first and last telemetry locations within a 24-hour monitoring session. All hourly or bihourly movements less than or equal to 150 metres were counted as zero metres to account for telemetry error and to avoid exaggerating hourly and daily movement distances (Theuerkauf and Jedrzejewski 2002).

Prior to analysis, I divided data into biological seasons for each species. Wolf seasons were defined as denning/rendezvous (April 15 to August 31) and fall/winter (September 1 through April 14). Bear seasons were defined as spring (den emergence to July 14), berry (July 15 to September 14) and pre-denning (September 15 to den entry) to coincide with major changes in food type and availability and associated behaviour.

I divided black bear data into one of two behavioural classes based on expert opinion (field staff and National Park Wardens) of established bear behaviour around humans. Bears that were known to be shy around humans and areas of

high human-use were considered to be "wary". Bears that were used to being approached or harassed by humans were considered "habituated" or conditioned to human presence (Herrero 1985).

I separated monitoring data by species, biological season, sex and habituation status (black bears only), and in the case of wolves, by pack. I analysed wolves separately due to the dramatic differences in prey availability within each packs home range (Banff National Park, unpublished data). To limit the number of tests, I grouped telemetry data into four daylight periods using sunrise/sunset tables (Herzberg Institute of Astrophysics, National Research Council, Victoria, B.C.). Dawn covered the two hour period extending from one hour before sunrise to one hour after sunrise; day occurred from one hour after sunrise to one hour before sunset; dusk occurred from one hour before sunset to one hour after sunset; and night occurred from one hour after sunset to one hour before sunrise. Length of daylight varied between 7.88 and 16.58 hours, and night varied from 9.2 to 18.1 hours in length. Crepuscular periods varied by 14 minutes throughout the year, and for simplicity of analysis I did not account for this variation.

Statistical Analysis

All data were non-normal with unequal sample sizes and unequal variances and could not be normalised with logarithmic or square root transformations. I compared hourly and daily movement rates within species and groups using either

the Kruskal-Wallis test, or in the case of two groups, the Mann-Whitney U test (SYSTAT 10.0). I used a normal approximation method for determining the significance of Mann-Whitney U tests when group size exceeded 40 (Zar 1999). I used non-parametric post-hoc multiple comparison tests to determine where differences occurred within significant Kruskal-Wallis tests (Dunns test for unequal sample sizes) (Zar 1999).

To determine whether pup-rearing activities influenced the movement patterns of wolf M1, I compared wolf M1's hourly movement rates in each daylight period during the denning/rendezvous period of 2000 (a non-litter year) with those during the denning/rendezvous period of 2001 (a litter year) using a series of Mann-Whitney U tests.

To examine temporal use of habitat within and adjacent to designated wildlife corridors and areas of high human use, I created a digital layer of high human-use areas and wildlife corridors using Arcview 3.2. I superimposed the 24-hour telemetry data on this layer and selected all data points occurring within 250 metres of a wildlife corridor or high human-use feature. This distance was chosen to account for telemetry error and to provide an additional 100-metre buffer to account for residual human activity on the outskirts of the high human-use features. In addition, exact boundaries of wildlife corridors are difficult to define, therefore the buffer zone captures points within the greater corridor region. I divided the resulting data by species, wolf pack, habituation status (for black

bears only) and season. For this analysis I used two seasons only, to correspond to the high and low human-use seasons in the park, and to the seasonal operations of outlying resorts. I defined summer as May 15 through September 30, and winter as October 1 through May 14. Daylight at time of telemetry location was determined with sunrise/sunset tables following the procedure outlined above, and I combined dawn and dusk into one "twilight" class. I compared the observed and expected frequency of day, night and twilight locations within and immediately adjacent to wildlife corridors and areas of high human-use using a G-test for goodness of fit (Zar 1999). The expected distribution was equal to the distribution of all 24-hour data across the three light periods (i.e. the availability of the three light periods) in each season.

RESULTS

A total of 249 24-hour monitoring sessions were conducted during the study period (117 wolf, 105 black bear, and 27 grizzly bear).

Daily Movement Patterns

Wolves

During the fall/winter season, wolf M1 showed peaks in movement between 08:00 and 10:00 and at 15:00, with a pronounced rest period at approximately 13:00. Movement at night was low with a pronounced drop between 22:00 and 07:00 (Figure 3-2a). There were significant differences in the hourly movement

rates of wolf M1 across daylight periods during fall/winter season ($H = 48.707$; df = 3; $P < 0.0001$). Night hourly movements were significantly lower than dawn ($Q = 4.341$; $k = 4$; $P < 0.001$), day ($Q = 5.757$; $k = 4$; $P < 0.0001$), and dusk ($Q = 3.113$; $k = 4$; $P = 0.01$) movements. There were no significant differences between dawn, dusk and daytime hourly movements (Table 3-1).

During the denning/rendezvous season, wolf M1's movements were low between 07:00 and 20:00. A peak in activity occurred between 01:00 and 06:00 (Figure 3-2b). There were significant differences in the hourly movement rates of wolf M1 across daylight periods during denning/rendezvous season ($H = 21.277$; df = 3; $P = 0.0001$). Day movements were significantly lower than night movements ($Q = 3.368$; $k = 4$; $P = 0.005$), and dusk movements ($Q = 3.001$; $k = 4$; $P = 0.015$). There were no differences between dawn, dusk and night hourly movements (Table 3-1).

During the fall/winter season, wolf M2 showed a peak in activity between 06:00 and 10:00. Activity was lowest in mid day at approximately 13:00. M2 showed moderate activity between 14:00 and 00:00, with a low at 01:00. Movement then steadily increased through the night until the morning peak (Figure 3-2c). There were significant differences in the hourly movement rates of wolf M2 across daylight periods during fall/winter season ($H = 10.88$; df = 3; $P = 0.01$). Dawn movement rates were significantly higher than day movements ($Q = 3.105$; $k = 4$; $P = 0.015$) and night movements ($Q = 2.672$; $k = 4$; $P = 0.047$). Dusk movements

were higher than night and day movements and lower than dawn movements, although these differences were not statistically significant (Table 3-1).

During the denning/rendezvous season, wolf M2 showed a peak in activity at approximately 04:00. Night movements were relatively high with little movement during the afternoon. Movement generally increased at approximately 20:00 (Figure 3-2d). There were no significant differences in the hourly movement rates of wolf M2 across daylight periods during denning/rendezvous season ($H = 6.18$; df = 3; $P = 0.103$) likely as a result of low sample sizes. M2's movement rates were highest during dusk, followed by night, day, and dawn (Table 3-1).

For wolf M1, daytime hourly movement rates during the fall/winter season were significantly higher than during the denning/rendezvous season ($U = 26795.5$, $n_1 = 196$; $n_2 = 402$; $Z = 6.354$; $P < 0.001$), and night-time hourly movement rates were significantly higher during the denning/rendezvous season than during the fall/winter season ($U = 33077$; $n_1 = 91$; $n_2 = 628$; $Z = 2.432$; $P < 0.015$). Dawn and dusk movement rates were similar between seasons.

For wolf M2, there were no significant differences in movement rates within each daylight period during the denning/rendezvous versus the fall/winter seasons, possibly due to the small sample size of denning/rendezvous period data.

The median hourly distance moved by wolf M1 was 200 m/hr (range 0 m to 11,461 metres), and his median minimum daily distance moved was 11,908 m/day (range 1,745 m to 47,963 metres). M1's median minimum daily movement distance during denning/rendezvous season (17,256 m/day) was greater than that during the fall/winter season (11,081 m/day), although the difference was not significant.

The median hourly distance moved by wolf M2 was 224 metres (range 0 to 3,678 m/hr), and his median minimum daily distance moved was 11,621 metres (range 6,242 m to 25,250 m). The median minimum daily distance travelled during denning season (9,307 m/day) was lower than that during fall/winter season (12,570 m/day), however the paucity of denning period monitoring sessions precluded a statistical test for significance.

Daily travel during the denning/rendezvous period was higher for M1 than for M2 although this difference could not be statistically tested, again due to the low sample size of M2 denning season data. There was no significant difference between the minimum daily movement distances of M1 and M2 during the fall/winter period.

In comparing between dawn, day, dusk, and night hourly movement rates of wolf M1 during the litter year (2001) versus the non-litter year (2000), I found no

significant difference between years, suggesting that denning/rendezvous season movement rates remain stable regardless of the presence of pups.

Wary Black Bears

In spring, movements of wary black bears (n = 12) were low during night hours, with movement increasing at approximately 10:00. Movement was fairly consistent during the daylight hours, and decreased at 21:00. A subtle decrease in movement between 11:00 and 14:00 may indicate a late morning/early afternoon rest period (Figure 3-3a). There were significant differences in hourly movement rates of wary bears across daylight periods ($H = 115.97$; df =3; $P < 0.001$). Day ($Q = 9.803$; $k = 4$; $P < 0.0001$) and dusk movements ($Q = 7.307$; $k = 4$; $P < 0.001$) were significantly greater than night movements, and day ($Q = 3.867$; $k = 4$; $P < 0.001$) and dusk movements ($Q = 4.148$; $k = 4$; $P < 0.001$) were significantly greater than dawn movements. Night and dawn movements were statistically similar, and day and dusk movements were similar (Table 3-1).

During the berry season, movement rates of wary black bears rose at 05:00 and remained stable during the day. Movement decreased at approximately 19:00 and remained low throughout the night (Figure 3-3b). There were significant differences in the hourly movement rates of wary bears across daylight periods during berry season ($H = 150.923$; df = 3; $P < 0.0001$;). Dawn, day, and dusk movements were equal, but significantly greater than night movements (Q_{dawn} =

4.756, $k = 4$, $P < 0.001$; $Q_{day} = 11.954$, $k = 4$, $P < 0.001$; $Q_{dusk} = 6.972$, $k = 4$, $P < 0.001$) (Table 3-1).

During the pre-denning season, movements of wary black bears were relatively consistent during the day and night, with slightly higher movement rates during daylight hours (Figure 3-3c). There were no significant differences in dawn, day, dusk, and night movements of wary bears during the pre-denning season (Table 3-1).

Habituated Black Bears

In spring, movement rates of habituated black bears (n = 6) remained low during night hours, rose at 09:00, and remained relatively stable throughout the day. Movement decreased at approximately 22:00 (Figure 3-4a). For habituated black bears, there were significant differences in hourly movement rates across daylight periods during the greenup/spring season ($H = 49.563$; df = 3; $P < 0.0001$). Hourly movements during day and dusk were similar, but were significantly higher than movement rates during the night ($Q_{day} = 6.488$, $k = 4$, $P < 0.001$; $Q_{dusk} = 4.370$, $k = 4$, $P < 0.001$). Dawn movement rates were higher than night movement rates although this difference was not significant (Table 3-1).

During the berry season, habituated bears moved little during the night hours, and increased their movement rates between 05:00 and 09:00. Movement remained quite stable during the daylight hours, and decreased again at approximately

21:00, remaining low throughout the night (Figure 3-4b). During berry season, there were significant differences in hourly movement rates of habituated bears across daylight periods ($H = 74.553$; df = 3; $P < 0.0001$). Hourly movement rates during dawn, daylight and dusk were statistically similar, but were significantly higher than night movement rates ($Q_{dawn} = 5.330$, $k = 4$, $P < 0.001$; $Q_{day} = 8.190$, $k = 4$, $P < 0.0001$; $Q_{dusk} = 3.407$, $k = 4$, $P = 0.004$) (Table 3-1).

During the pre-denning season, habituated bears were relatively inactive at night, with movement rates increasing at approximately 09:00. Movement remained high throughout the daylight hours, and decreased again at approximately 22:00 (Figure 3-4c). There were significant differences in hourly movement rates across daylight periods for habituated bears during the pre-denning season ($H = 35.379$; df = 3; $P < 0.0001$). Dusk ($Q = 2.966$; $k = 4$; $P = 0.018$) and daytime movements ($Q = 5.629$; $k = 4$; $P < 0.001$) were significantly higher than night movements. Dawn movements were higher than night movements, although the difference was not significant (Table 3-1).

There were no significant differences between male and female black bear daily movement distances within seasons, and no significant differences between habituated and wary black bear daily movement distances within seasons. Overall, daily movement distance for all black bears was lowest during the pre-denning season (median 5,824 m/day), followed by spring (median 5,889 m/day),

and was highest during the berry season (median 7,276 m/day), although these differences were not statistically significant.

Grizzly Bears

In spring, grizzly bear movement rates rose between 04:00 and 07:00, then declined between 08:00 and 13:00, possibly indicating a morning/early afternoon rest period. Movements remained low throughout most of the day, increasing again at approximately 18:00. Movement decreased at approximately 23:00 for the night (Figure 3-5a). During spring/greenup season, there were significant differences in grizzly bear hourly movement rates across daylight periods (H = 9.86; d.f. = 3; P = 0.02), although post-hoc tests failed to detect these differences, possibly due to low sample size. Hourly movement was highest during dawn and dusk, and lowest during night. Daytime movements were higher than night movements, but lower than dawn and dusk movements (Table 3-1).

During berry season, grizzlies had low movement rates throughout the night, and became more mobile from approximately 08:00 to 11:00. Movements decreased between 12:00 and 14:00, possibly indicating an early afternoon rest period. A small increase in movement was noted at approximately 16:00, followed by a general decline in movement until morning (Figure 3-5b). During berry season, there were significant differences in hourly movement rates across daylight periods (H = 18.75; df = 3; P = 0.0003), but again, post-hoc tests were

inconclusive in identifying differences. Daytime movements were highest, followed by dusk and night. Dawn movements were lowest (Table 3-1).

During the pre-denning season, grizzly bear movement was relatively consistent throughout the day, with no significant difference in hourly movement rates across daylight periods (Figure 3-5c) (Table 3-1).

The median hourly travel-rate for grizzlies averaged over the bear year was 180 m/hr (range 0 m/hr to 3,154 m/hr). Male and female grizzly bears had similar movement rates in each of the four daylight periods. As both female bears were considered to be habituated, and the lone male bear was considered to be wary, it can also be suggested that there were no significant differences in hourly movement rates of habituated and wary grizzly bears.

Daily movement distances of grizzlies ranged from 0 to 17,422 m/day (median 5,726 m/day). There were no significant differences in daily movement distance across seasons for both male and female grizzly bears, and hence, no difference in daily movement distances across seasons for wary or habituated grizzly bears.

Temporal Movement Patterns around Wildlife Corridors and Areas of High Human Use

Wolves

Twenty-three summer locations and 45 winter locations of wolf M2 occurred in or immediately adjacent to wildlife corridors. There was no significant difference in the temporal distribution of locations within wildlife corridors relative to that of the surrounding landscape. For wolf M1 of the Bow Valley pack, four summer locations and four winter locations occurred in or immediately adjacent to wildlife corridors. The paucity of data precluded statistical analysis, however all summer corridor locations and all but one winter corridor location occurred during daylight hours. The fourth winter corridor location occurred at night.

During the summer season, I did not document any use of habitat within or immediately adjacent to high day-use areas by wolf M1 or M2. In winter, 46 locations of M2 occurred within or adjacent to high day-use areas (golf course, campgrounds and ski hills), and 40 locations occurred within or adjacent to town perimeters (Banff and Canmore). Wolf M2 used high day-use areas significantly more often at night and less often during daylight and twilight than the surrounding landscape ($G = 13.812$; df = 2; $P = 0.001$). Wolf M2 also used habitat within town site perimeters significantly more often at night and less often during daylight and twilight than the surrounding landscape ($G = 36.94$; df = 2; $P < 0.0001$). Ninety percent of all locations within or adjacent to town perimeters occurred at night.

In winter, wolf M1 used habitat adjacent to or within high day-use areas significantly more often at night and less often during daylight and twilight than expected ($G = 14.734$; df = 2; $P = 0.0006$). There were no documented cases of wolf M1 using habitat adjacent to or within town perimeters during winter or summer months.

During the summer season, wolf M1 used habitat adjacent to outlying resorts significantly more often at night and less often during the day than expected ($G = 12.263$; df = 2; $P = 0.002$).

Black Bears

During summer, habituated black bear use of habitat within or adjacent to areas of high human-use (campgrounds, high day-use areas, and resorts) (n = 15) and wildlife corridors (n = 9) was not significantly different from their use of the surrounding landscape. Use of habitat within or directly adjacent to a town site (Lake Louise) by habituated bears was documented on six occasions, all during daylight hours.

Wary bears were not located within or immediately adjacent to town sites during this study. Similar to their habituated counterparts, the temporal use of habitat adjacent to areas of high human use by wary black bears was not significantly different than that of the surrounding landscape. The temporal use of wildlife corridors by wary black bears was significantly different than their use of the

surrounding landscape ($G = 6.458$; df = 2; $P = 0.04$), with less use during daylight, and more use during night and twilight than expected. During summer, all ten instances of wary black bears using ski areas occurred during daylight.

Grizzly Bears

All instances of grizzly bear use of habitat within or adjacent to high human-use areas involved the two habituated female bears. In these cases, their temporal use of high human-use areas was not significantly different than that of the surrounding landscape. Similarly, all grizzly bear use of wildlife corridors involved the two habituated females, however their temporal use of wildlife corridors was significantly different from that of the surrounding landscape ($G = 18.96$; df = 2; $P = 0.0001$). Grizzlies used wildlife corridors significantly less during the day and more during the night and twilight than expected. Ski hill use was only documented on two occasions, both during daylight hours.

DISCUSSION

Wolves

One of the most striking results of this study was the shift in daily movement patterns between denning/rendezvous season and fall/winter season, particularly for wolf M1. During fall/winter, M1's movements were primarily diurnal and crepuscular, but during denning season his movements shifted to nocturnal and crepuscular. A number of studies have documented diurnal movement in denning wolves (Mech and Merrill 1998; Murie 1944; Harrington and Mech 1982). In

Banff National Park, backcountry spring and summer monitoring of the Spray River (Coscia 1990) and the Cascade River (Parks Canada, unpublished data) wolf packs indicated daytime movement away from the den-site, including hunting activity. Similar to my results, Ballard et al. (1991) found that an alpha male wolf in south central Alaska often left the densite at dusk and returned at dawn, however average time away from the den was 30 to 36 hours.

In Banff, it is possible that wolves remain at the den/rendezvous site during daylight hours to guard pups against diurnal predators such as black and grizzly bears. If this were the case, we would expect to see wolves moving throughout daylight hours during the denning/rendezvous season in years when pups are not produced. However, my data indicate that movement rates in the four daylight periods were similar in denning years and non-denning years, suggesting that activities related to pup rearing are not likely responsible for the lower diurnal movements during the denning/rendezvous season.

High summertime temperatures may also influence the daily movement patterns of animals. Kolenosky and Johnston (1967), however, noted that in temperatures as hot as 32° C, Ontario wolves travelled during daylight hours and into dusk, suggesting that ambient temperature had little effect on wolf movements in their study. Summer temperatures in Banff National Park are characterised as relatively cool with daytime highs rarely exceeding 25° C, therefore summer

daytime temperatures are unlikely to influence wolf movement patterns in the Bow Valley.

Another possible explanation for the difference in daily patterns between the two seasons is prey activity patterns. I did not collect data on prey activity patterns in BNP. Elk are the primary prey species of wolves in the Bow Valley on a year round basis (Paquet 1993; Hebblewhite 2000), and daily activity patterns of elk in the central Rocky mountains show a consistent bimodal pattern throughout the year, with peaks in activity occurring at dawn and dusk (J. Frair, unpublished data). In addition, the visual system of wolves is most efficient in low daylight and crepuscular light levels (Harrington 1996), so to maximise hunting efficiency, one would expect wolves to hunt and move primarily during daylight or crepuscular hours in all seasons.

I suggest that the nocturnal and crepuscular movement pattern seen by wolves in the Bow Valley during the denning/rendezvous season may be the result of very high daytime human use in BNP during summer months. Vila et al. (1995) found that Iberian wolves in Northwest Spain were active mostly at night, followed by crepuscular hours, with daytime activity being the lowest, and suggested this pattern was an adaptation by wolves to avoid contact with humans. Similarly, Cucci et al. (1997) found that wolves in Italy were primarily nocturnal with little or no activity during daylight hours, and also attributed wolf nocturnal patterns as

a strategy to minimise contact with humans. Such strategies may not be necessary in the Bow Valley during winter months when human use is relatively low.

Minimum daily movement distances by wolves in this study ranged from 1.7 to 48 km and averaged just over 11 km. Jedrzejewski et al. (2001) noted that daily movement distances varied seasonally for wolves in Poland, although in their study, the highest daily movements occurred in winter and the lowest occurred during denning season, the opposite of my results for wolf M1. They reported that daily movement distance increased as prey densities decreased, which may account for such high daily movement distances for wolf M1 during denning season, when the pack's primary prey, elk, were concentrated around the town of Banff.

Both the Fairholme and Bow Valley wolf packs appear to use temporal resource partitioning to access habitat in close proximity to human activity, navigating through these areas primarily during night and crepuscular hours. Temporal use of wildlife corridors was similar to that of the surrounding landscape for wolf M2 in both summer and winter seasons. A paucity of data precluded such analysis for wolf M1, however, seven of eight data points occurring within wildlife corridors occurred during daylight hours. All occurrences of wolves moving through the perimeter of town sites (Banff and Canmore) occurred at night, and only during winter months. Nocturnal and cryptic behaviour has also been documented in

Italy (Cucci et al. 1997), and Spain (Vila et al. 1995), where wolves exist in areas where human densities are high.

Black Bears

Both behavioural classes of black bears had similar daily movement patterns during spring/greenup season and berry season. During spring/greenup, bears moved most during daytime and dusk, and least during night and dawn. During the berry season, bears were primarily crepuscular and diurnal. During the pre-denning season, however, wary bears moved equally in all daylight periods, but habituated bears moved the greatest distances during day and dusk. The constant movement by wary bears during pre-denning could be due to their heightened demand for food resources during hyperphagia.

Similar to my results, Garshelis and Pelton (1980), found that black bears in North Carolina were more crepuscular during spring, more diurnal during berry season, and showed extensive nocturnal activity in fall which they attributed to hyperphagia. Amstrup and Beecham (1976) and Lariviere et al. (1994) both report diurnal and crepuscular tendencies in Idaho and Quebec, respectively.

Male and female black bears in my study had similar minimum daily movement distances in each season, as did habituated and non-habituated black bears. Minimum daily movement distances were statistically similar in all seasons.

Garshelis et al. (1983) found that adult male black bears travelled greater daily distances than did adult females, and reported that in only one of their three study areas did they detect seasonal differences in daily movement distances. Amstrup and Beecham (1976) found that daily movements increased when food was sparse. The mean minimum daily movement distance for their black bears in Idaho was 1.3 km, somewhat lower than the 6.4 km for Bow Valley bears. Garshelis and Pelton (1980) suggest that bears require daylight to optimally select berries from bushes, possibly explaining the high diurnal movement rates during berry season in the Bow Valley. Lariviere et al. (1994) and Reimchen (1998) also attributed diurnal movements to more efficient foraging and travelling in daylight conditions.

Neither wary nor habituated black bears showed a temporal pattern in their use of habitat adjacent to areas of high human use, and may use vegetative security cover to remain cryptic while utilising these areas. Habituated black bears showed no temporal pattern in their use of wildlife corridors, however wary black bears used corridors less during daylight hours and more during night and twilight than expected.

McCutchen (1990) found that although black bears in Rocky Mountain National Park had home ranges in areas of high human-use, wary bears were secretive and avoided humans and developed areas, while habituated bears were found closer to areas of high human activity and human facilities.

Grizzly Bears

In spring, grizzly bears were mainly crepuscular, with low movement during the day, and very low movement at night. During berry season, daytime movements were highest, followed by dusk and night movements. As with black bears, the higher diurnal movements by grizzlies in berry season may be explained by their need to use eyesight to optimally forage on berries. Hourly movement rates were equal across daylight periods during the pre-denning season, as was the case with wary black bears in our study area, suggesting that grizzlies forage throughout the day and night periods, likely due to hyperphagia.

Olson et al. (1998) found that brown bears in Alaska had diurnal activity patterns where human use was non-existent, and crepuscular activity where human use was high. Gunther (1990) found that grizzlies in Yellowstone had crepuscular activity peaks in an area frequented by hikers, campers and horse parties, with very little activity during mid-day when human use was highest. Bjarvall and Sandegren (1987), however, report a diurnal activity pattern in their study bear, and suggest that this pattern is likely typical of undisturbed populations.

In my study, male and female grizzly bears had similar hourly movement rates within each of the four daylight periods, and similar daily movement rates in each season. The daily movement distances of my bears (0 m to 17.4 km) were comparable to those of Clevenger et al. (1990) (100 m to over 20 km), however, their bears travelled furthest in June/July and least during the pre-denning season, whereas my bears showed no seasonal differences in daily movement. Similar to

my results, Roth (1983) found no significant seasonal trends in activity of brown bears in Italy, however, Weber (1987), found that maximum mobility of Romanian brown bears was related to hyperphagia.

All grizzly bear use of wildlife corridors and high human-use areas involved habituated individuals. Habitat within and adjacent to campgrounds and resorts was visited during the day and night, likely due to the prevalence of buffaloberry (*Shepherdia canadensis*) in these areas. Wildlife corridor use occurred primarily during night and twilight. Some temporal resource partitioning may be occurring in habituated grizzly bears, and habitat avoidance may be occurring in wary grizzlies around areas of high human activity. Gunther (1990) found that grizzlies in Yellowstone avoided habitat within 400 metres of campsites when occupied by humans, and used more open habitat and ranged further from tree cover when temporal restrictions to human use were implemented. Gunther (1990) supported such initiatives as a means of balancing grizzly bear needs while still allowing for visitor enjoyment.

Study Limitations

This study represents preliminary work into the spatio-temporal activity patterns of wolves, black bears and grizzly bears in the Bow Valley of Banff National Park. There were limitations to this study, the first being the lack of both a spatial and temporal (between years) habitat component. This element would have been

beneficial for analysis of bear movements as food availability and abundance may play a significant role in dictating movements. Second, due to the wide variation in location, habitat, and environmental conditions of comparative studies, it would have been extremely beneficial to have conducted simultaneous monitoring of collared bears and wolves in a control environment in Banff National Park (i.e. no or very low human use). A third limitation of this study is the paucity of data for wolf M2 during the denning/rendezvous season due to a late capture date. In general, summer wolf and grizzly bear data was scarce relative to black bear data, as a result of the smaller number of animals collared, and due to their periodic absence from the valley.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

In summary, I found that wolves moved during crepuscular hours and daylight when human use in the valley was low. During late spring and summer months, however, when human use is very high, they reverted to a nocturnal and crepuscular movement pattern, with very low movement rates during daylight. This pattern is not typical of wolves in other study areas, and is not likely the result of daytime temperatures or limitations associated with pup-raising activities. Wolf movement through wildlife corridors occurred during day, night and twilight, suggesting the importance of human use guidelines for corridors. Wolf movement through areas of high human-use, including campgrounds and high day-use areas occurred only during night hours in winter months.

The diurnal and crepuscular movement pattern exhibited by black and grizzly bears may be related to the relationship between sightability and optimal foraging. The heightened nocturnal activity in grizzly and wary black bears during the pre-denning period may be the result of the increased foraging drive associated with hyperphagia. Black bears appeared to be less affected temporally by areas of high human use than were wolves and wary grizzlies, although they may use vegetative security cover to remain cryptic in these environments.

1. Crepuscular and night activity was documented in all three focal species particularly when navigating through areas of high human activity or during months when human use of the valley is high. This pattern suggests temporal displacement from habitat may be occurring as a result of human activity. To increase habitat effectiveness for large carnivores during crepuscular and night hours, I recommend that human activity outside the footprints of town sites, campgrounds and outlying commercial accommodation areas be limited to daylight hours.

2. Use of wildlife corridors occurred primarily during night and crepuscular hours for wary black bears and grizzly bears, however wolves often used wildlife corridors during daylight hours. I recommend limiting human use of wildlife corridors throughout all hours of the day and night to maintain habitat effectiveness of these important linkage zones and to allow for unimpeded movement of wary species.

3. Diurnal movements are typical of bears during spring, summer and fall months, and are typical of wolves during winter. These species likely use vegetative cover to remain cryptic throughout daylight hours in the Bow Valley, and may utilise areas where they are least likely to be disturbed. The spatial predictability of human activity may be important to wildlife, particularly the more wary species. I recommend that off-trail recreational activity be discouraged to ensure that diurnal wildlife movements are not interrupted by spatially unpredictable human disturbance. Within a management context, I recommend that casual and organised (i.e. eco-tourist groups) be limited to using existing trails for both summer and winter activities (e.g. hiking and snowshoeing).

4. My data suggest that wolves occupying a home range west of the town of Banff travelled extensively throughout daylight hours during winter months. Any increase in human use of wolf habitat during winter months may cause wolf movement patterns to become more nocturnal, similar to movement patterns during high human use (summer) months. I recommend capping the temporal use of existing developments or human-use facilities outside of town boundaries at current levels.

LITERATURE CITED

Alkon, P.U. and D. Saltz. 1988. Influence of season and moonlight on temporal activity patterns of Indian-crested Porcupines (*Hystrix indica*). *J. Mamm.* 69(1): 71-80.

Amstrup, S.C., and J. Beecham. 1976. Activity patterns of radio-collared black bears in Idaho. *J. Wildl. Manage.* 40(2): 340-348.

Andelt, W.F, and P.S. Gipson. 1979. Home range, activity and daily movements of coyotes. *J. Wildl. Manage.* 43(4): p.944-51

Ayres, L., L.S. Chow, and D.M. Graber. 1986. Black bear activity patterns and human induced modifications in Sequoia National Park. *Int. Conf. Bear Res. and Manage.* 6: 151-154.

Ballard, W.B., L.A. Ayres, C.L. Gardner, and J.W. Foster. 1991. Den site activity patterns of gray wolves, Canis lupus, in southcentral Alaska. *Canadian Field Naturalist* 105(4): 497-504.

Bjarvall, A. and F. Sandegren, 1987. Early experiences with the first radio marked brown bears in Sweden. *Int. Conf. Bear Res. and Manage.* 7: 9 -12.

Brandenburg, D.M. 1996. Effects of roads on behavior and survival of black bears in coastal North Carolina. M.Sc. Thesis. Univ. of Tennessee, Knoxville. 130pp.

Callaghan, C.J. 2002. The ecology of gray wolf (Canis lupus) habitat use, survival and persistence in the Central Rocky Mountains, Canada. Ph.D. Dissertation. University of Guelph, Ontario. 211 pp.

Clevenger, A.P. 1993. Pine marten (Martes martes L.) home ranges and activity patterns on the island of Minorca, Spain. *Z. Säugetierkunde* 58: 137-143.

Clevenger, A.P., Purroy, F.J., and M.R. Pelton. 1990. Movement and activity patterns of a European brown bear in the Cantabrian Mountains, Spain. *Int. Conf. Bear Res. and Manage.* 8:205-211.

Cornwell, L., C. Pacas and J. Green. 1996. Introduction: Ecological Outlooks for the Banff Bow Valley. Chapter 1 in: Green, J., C. Pacas, L. Cornwell and S. Bayley (eds). Ecological Outlooks Project. A Cumulative Effects Assessment and Futures Outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, ON. 20 pp.

Coscia, E.M. 1990. Homesite monitoring of a wolf pack in Banff National Park. Research Report: May - July 1990. 27pp.

Cuicci, P., L. Boitani, F. Francisci, and G. Andreoli. 1997. Home range, activity and movements of a wolf pack in central Italy. *J. Zool., Lond.* 243: 803 - 819.

Daan, S. 1981. Adaptive daily strategies in behavior. *Handb. Behav. Neurobiol.* 4: 275-278.

Drew, G.S., and J.A. Bissonette. 1997. Winter activity patterns of American martens: rejection of the hypothesis of thermal-cost minimization. *Can. J. Zool.* 75: 812-816.

Garshelis, D.L., and M.R. Pelton. 1980. Activity of black bears in the Great Smoky Mountains National Park. *J. Mamm.* 61(1): 8-19.

Garshelis, D.L., H.B.Quigley, C.R. Villarrubia, and M.R. Pelton. 1983. Diel movements of black bears in the southern Appalachians. *Int. Conf. Bear Res. And Manage.* 5: 11-19.

Gibeau, M.L. 2000. A conservation biology approach to management of grizzly bears in Banff National Park, Alberta. Ph.D. Dissertation, University of Calgary, Alberta.

Griffiths, M. and C.P. Van Schaik. 1993. The impact of human traffic on the abundance and activity periods of Sumatran rainforest wildlife. *Cons. Biol.* 7(3): 623-626.

Gunther, K.A. 1990. Visitor impact on grizzly bear activity in Pelican Valley, Yellowstone National Park. *Int. Conf. Bear Res. And Manage.* 8: 73-78.

Harrington, F.H. and L.D. Mech. 1982. Patterns of homesite attendance in two Minnesota wolf packs. In *Wolves of the World: Perspectives of Behavior, Ecology, and Conservation*: 81-105. Harrington, F.H., and P.C. Paquet (Eds). Park Ridge: Noyes Publishing Co.

Harrington, F.H. 1996. Wolf eyes and ears: a review of visual and auditory senses. P. 242-249 in: *Wolves of America Conference Proceedings*. Fascione, N. and M. Cecil (Eds).

Hebblewhite, M. 2000. Wolf and elk predator-prey dynamics in Banff National Park. M.Sc. Thesis. University of Montana. 130 pp.

Herrero, S. 1985. Bear attacks: their causes and avoidance. Nick Lyons Books, Winchester Press, Piscataway, New Jersey. 287 pp.

Holland, W.D. and G.M. Coen. 1983. Ecological (biophysical) land classification of Banff and Jasper National Parks. Volume III: The wildlife inventory. Can.Wildl. Serv., Edmonton. 691 pp.

Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska and H. Okarma. 2001. Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. *Can. J. Zool.* 79: 1993 - 2004.

Kolenosky, G.B., and D.H. Johnston. 1967. Radio-tracking timber wolves in Ontario. *Am. Zoologist* 7: 289-303.

Lariviere, S., J. Huot, and C. Samson. 1994. Daily activity patterns of female Black bears in a northern mixed-forest environment. *J. Mamm.* 75(3):613 - 620.

Lariviere, S. and F. Messier. 1997. Seasonal and daily activity patterns of striped skunks (*Mephitis mephitis*) in the Canadian prairies. *J. Zool., London.* 243: 255-262.

McCutchen, H.E. 1990. Cryptic behavior of black bears (*Ursus americanus*) in Rocky Mountain Ntl. Park, Colorado. *Int. Conf. Bear Res. And Manage.* 8: 65-72.

Mech, L.D. and S.B. Merrill. 1998. Daily departure and return patterns of wolves, *Canis lupus*, from at den at 80° N latitude. *Can. Field Nat.* 112: 515-517.

Murie, A. 1944. The wolves of Mount McKinley. University of Washington Press, Seattle. 238 pp.

Musiani, M., H. Okarma, and W. Jedrzejewski. 1998. Speed and actual distances traveled by radio-collared wolves in Bialowieza Primeval Forest (Poland). *Acta Theriologica* 43(4): 409-416.

Olson, T.L., Squibb, R.C., and B.K. Gilbert. 1998. Brown bear diurnal activity and human use: a comparison of two salmon streams. *Ursus* 10: 547-555.

Paquet, P.C., J. Wierzchowski, and C. Callaghan. 1996. Effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 in: Green, J., C. Pacas, L. Cornwell and S. Bayley (eds.). A Cumulative Effects Assessment and Futures Outlook for the Banff Bow Valley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, ON. 74pp.

Reimchen, T.E. 1998. Diurnal and nocturnal behavior of black bears, *Ursus americanus*, on bear trails. *Canadian Field-Naturalist* 112(4): 698-699.

Roth, H.U. 1983. Diel activity of a remnant population of European brown bears. *Int. Conf. Bear Res. and Manage.* 5: 223-229.

Roth, H.U. and D.H. Huber, 1986. Diel activity of brown bears in Plitvice Lakes National Park, Yugoslavia. *Int. Conf. Bear Res. and Manage*. 6: 177-181.

Serrouya, R. 1999. Permeability of the Trans Canada Highway to black bear movements in the Bow Valley of Banff National Park. M.Sc. Thesis. University of British Columbia.

Stelmock, J.J., and F.C. Dean. 1986. Brown bear activity and habitat use, Denali National Park - 1980. *Int. Conf. Bear Res. And Manage*. 6: 155-167.

Strang, C.A. 1983. Spatial and temporal activity patterns in two terrestrial turtles. *J. Herp.* 17(1): 43-47.

Theuerkauf, J. and W. Jedrzejewski. 2002. Accuracy of radio telemetry to estimate wolf activity and locations. *J. Wildl. Manage*. 66 (3): 859-864.

Van Dyke, F.G., Brocke, R.H., Shaw, H.G., Ackerman, B.B., Hemker, T.P., and F.J. Lindzey. 1986. Reactions of mountain lions to logging and human activity. *J. Wildl. Manage*. 50(1): 95-102.

Vila, C., Urios, V., and J. Castroviejo. 1995. Observations on the daily activity patterns in the Iberian wolf. p 335-340 in: *Ecology and conservation of wolves in a changing world.* Carbyn, L.N., Fritts, S.H., and D.R. Seip (Eds). Canadian Circumpolar Institute, Occasional Publication No. 35, 642 pp.

Warner, S.H. 1987. Visitor impact on brown bears, Admiralty Island, Alaska. *Int. Conf. Bear Res. Manage.* 7: 377-382.

Weber, P. 1987. Observations of brown bear movements in the Hargita Mountains, Romania. *Int. Conf. Bear Res. And Manage*. 7: 19-21.

White, G.C. and R.A. Garrott. 1990. Analysis of wildlife radio tracking data. Academic Press Inc. 383 pp.

Zar, J.H. 1999. Biostatistical Analysis. Fourth Edition. Prentice-Hall Inc. New Jersey. 663 pp.

Table 3-1: Hourly movement rates of radio-collared wolves, black bears and grizzly bears relative to daylight class.

	Distance Moved within each Daylight Period (m/hr)				
Species/ Season	**Dawn**	**Day**	**Dusk**	**Night**	**# Sessions**
Wolf M1 Fall/Winter	318	255	283	158	73
Wolf M1 Denning/Rend.	228	0	400	250	20
Wolf M2 Fall/Winter	667	200	269	224	21
Wolf M2 Denning/Rend.	79	190	510	231	3
Wary Black Bear Spring	160	250	354	90	33
Wary Black Bear Berry	301	343	333	103	33
Wary Black Bear Pre-Denning	158	177	246	168	8
Habit. Black Bear Spring	250	240	150	0	15
Habit. Black Bear Berry	293	285	214	79	10
Habit. Black Bear Pre-Denning	214	397	276	79	6
Grizzly Bear Spring	357	200	400	0	11
Grizzly Bear Berry	112	250	160	144	11
Grizzly Bear Pre-Denning	140	141	301	158	5

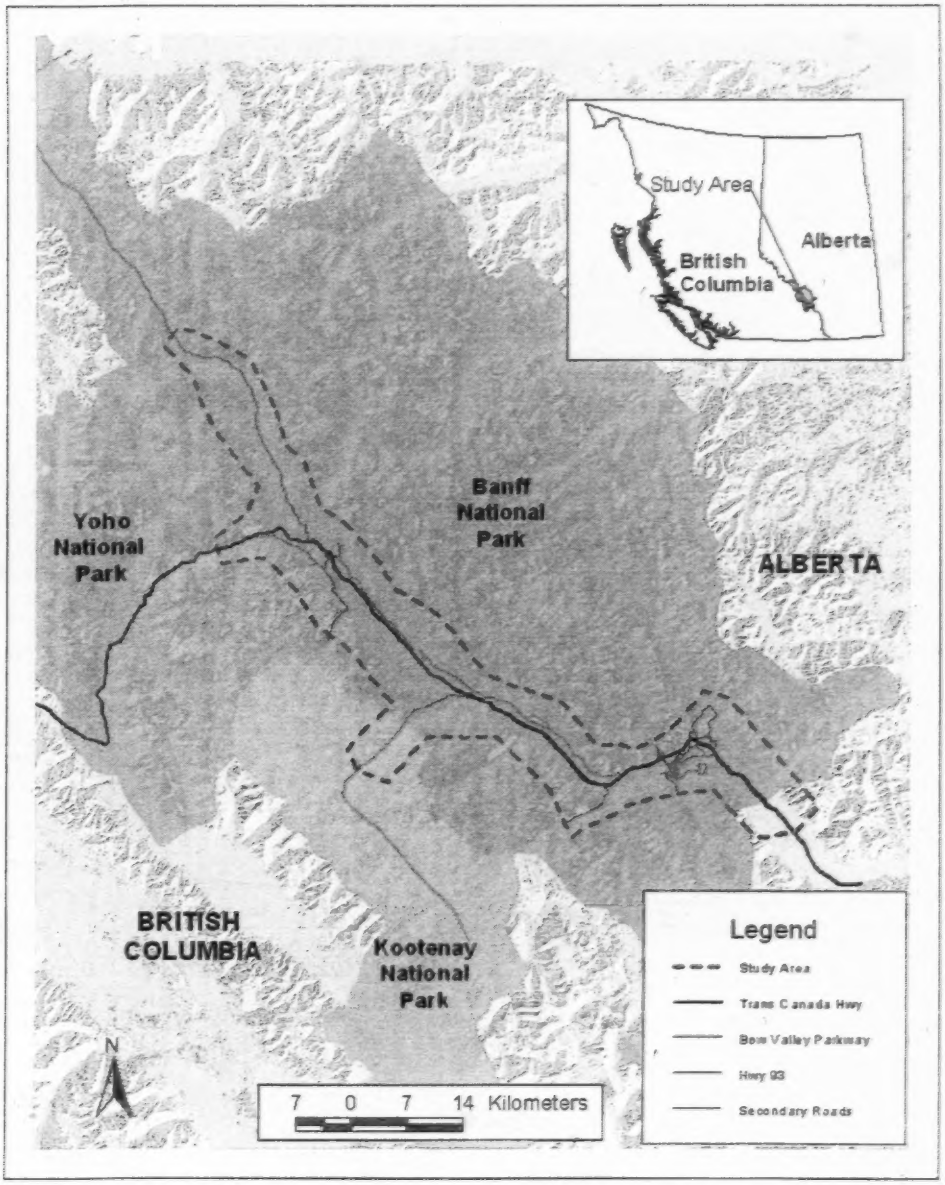

Figure 3-1: The greater Banff National Park region illustrating the study area.

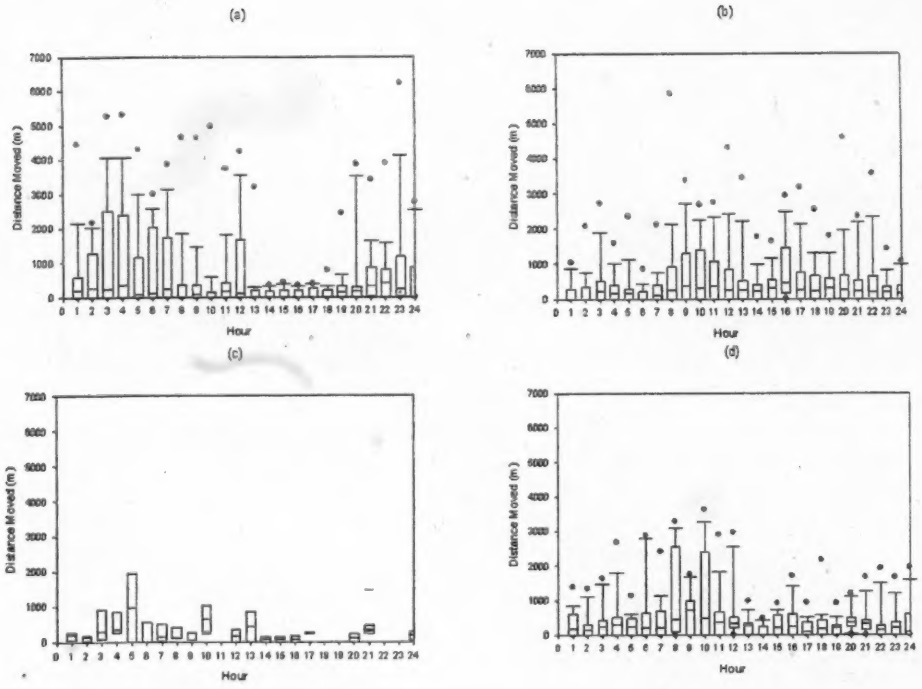

Figure 3-2: Hourly movement rates (m) of wolf M1 during (a) denning/ rendezvous season and (b) fall/winter season, and wolf M2 during (c) denning/ rendezvous season and (d) fall/winter season in the Bow Valley of Banff National Park. 1998 - 2001.

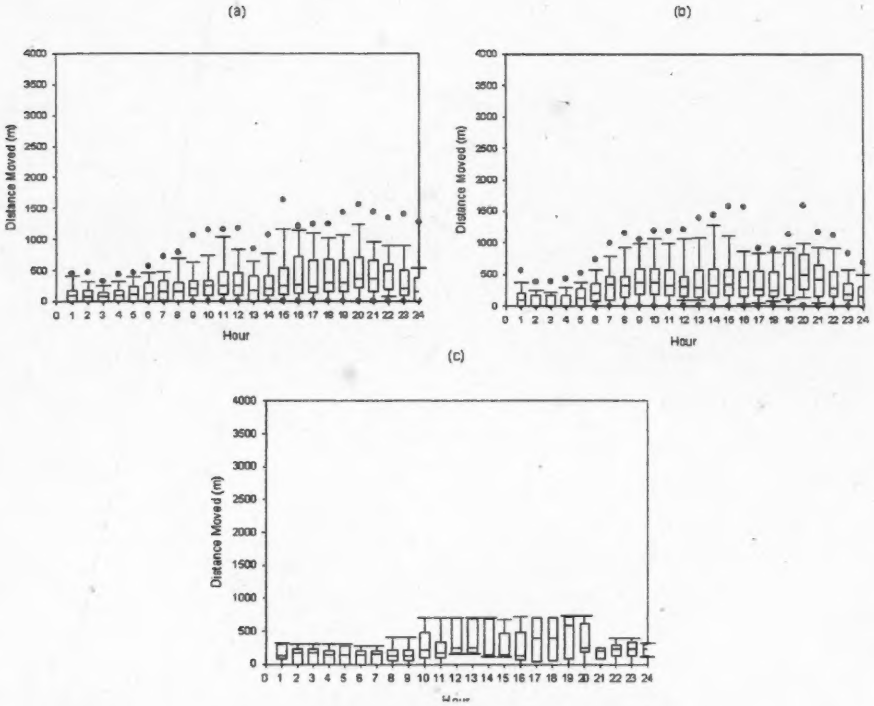

Figure 3-3: Hourly movement rates (m) of wary black bears in the Bow Valley of BNP during (a) spring, (b) berry season, and (c) pre-denning season. 1998 to 2001.

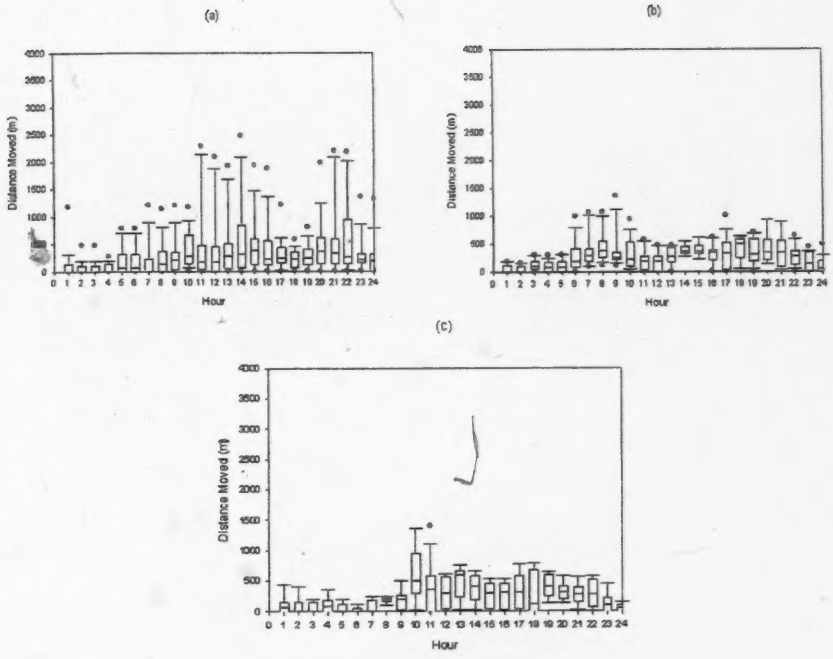

Figure 3-4: Hourly movement rates (m) of human-habituated black bears in the Bow Valley of BNP during (a) spring, (b) berry season, and (c) pre-denning season. 1998 to 2001.

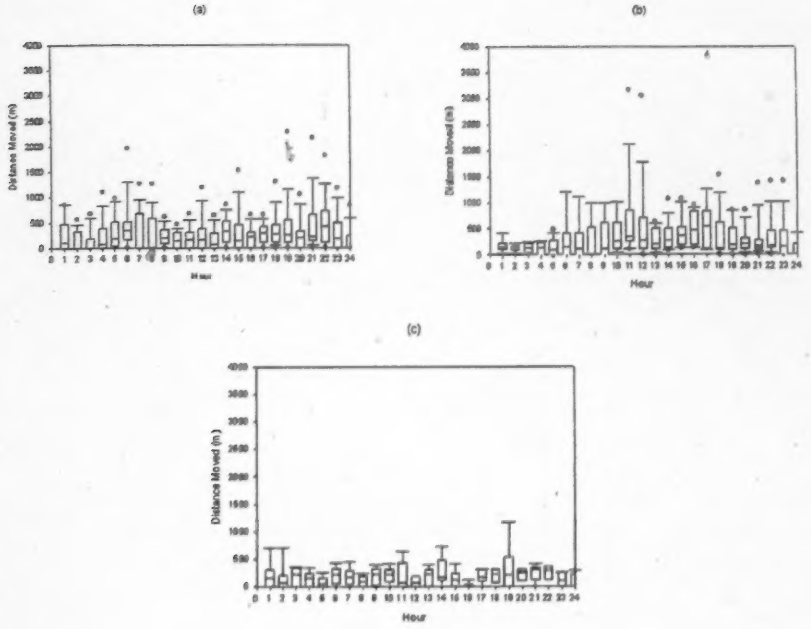

Figure 3-5: Hourly movement rates (m) of grizzly bears in the Bow Valley of BNP during (a) spring, (b) berry season, and (c) pre-denning season. 1998 to 2001.

CHAPTER 4

THE EFFICIENCY OF USING RADIO TELEMETRY TO ESTIMATE WOLF ROAD-CROSSING LOCATION AND FREQUENCY

INTRODUCTION

The effect of roads on gray wolves (*Canis lupus*) and other wide-ranging mammals continues to gain considerable ecological attention due to the rapid expansion of road networks that fragment natural landscapes (Noss et al. 1996; Forman 2000). In addition to contributing to direct mortality, roads may serve as barriers to daily and long-distance wolf movements, reducing landscape connectivity and threatening the persistence of sub-populations (Paquet et al. 1996; Alexander 2001; Callaghan 2002). Understanding wolf behaviour around roads can indicate the relative risk of direct mortality and changes in the degree of landscape permeability (Jaeger and Fahrig 2002). Furthermore spatial road crossing data may assist with planning mitigative measures to reduce the effects of roads on wolves, including construction of wildlife crossing structures, and the creation of slow speed zones to warn motorists of crossing "hot spots". Radio telemetry may be used to infer road-crossing location and frequency if conducted at appropriate temporal intervals. The objective of this study was to determine how length of time between consecutive radio-telemetry locations influences estimation of road-crossing frequency and location.

STUDY AREA

The study was conducted from May 1998 to March 2001 in the Bow River Valley of Banff National Park, located between 120 and 200 kilometres west of the city of Calgary, Alberta, in the Front and Main ranges of the Canadian Rocky Mountains (Figure 4-1). The park is approximately 6640 km^2 in area and is characterised by rugged mountainous topography. The Bow Valley ranges in width from approximately two to six kilometres, is oriented on a NW to SE axis, with valley-bottom elevations ranging from approximately 1330 to 2000 metres. Steep mountains and ridges provide natural fragmentation of the landscape, while annual visitation in excess of five million people (Cornwell et al. 1996) has subjected the landscape to extensive human-induced fragmentation.

Four major transportation corridors lie within the study area: the Trans Canada Highway (TCH), the Canadian Pacific Railway, Highway 93, and the Bow Valley Parkway (BVP). The average annual daily traffic volume for the TCH exceeds 14,500 vehicles, the BVP ranges in daily traffic volume from 55 to over 3500 vehicles, and Highway 93 ranges in traffic volume from 55 to over 7000 vehicles per day (Banff National Park, unpublished data). The westernmost 35 km of the TCH are two lanes wide and unfenced, while the balance of the TCH within the study area is four lanes wide and bounded by 2.4 metre high wildlife exclusion fences on either side. To increase highway permeability, 24 wildlife crossing structures and bridges (22 underpasses and 2 overpasses) are in place to facilitate wildlife movement across the highway (Clevenger and Waltho 2000). Numerous

secondary roads exist within the study area, primarily within the towns of Banff and Lake Louise, with isolated access roads facilitating travel to ski hills, campgrounds, and picnic areas.

METHODS

Data were collected from two wolves (the alpha male from the Bow Valley Pack [M1], and one adult male from the Fairholme Pack [M2]) between May 1998 and March 2001. Wolves were captured in modified steel foot-hold traps (toothed and padded No. 4 offset foot-hold traps, Livestock Protection Co., Alpine, TX), immobilised with Telazol™, and fitted with VHF radio-collars (Lotek Engineering, Newmarket, Ontario).

I monitored wolves from accessible roads in the study area using conventional radio-triangulation techniques (White and Garrott 1990). Telemetry bearings were plotted on 1:20,000 geo-corrected air photos with the use of a hand-held global positioning system (GPS) unit (Garmin 12XL, Garmin International Inc.) and wolf locations were recorded in UTM co-ordinates. Care was taken to avoid conducting telemetry in such close proximity to the wolves that we risked disturbing them and influencing their movements.

Conventional triangulation was used to assess average error, which was approximately ±150 metres, consistent with other telemetry-based research in

Banff National Park (Serrouya 1999; Hebblewhite 2000; Gibeau 2000; Callaghan 2002).

On an average of once per week, I conducted continuous 24-hour radio-telemetry monitoring sessions, obtaining one wolf location every hour for 24 consecutive hours (i.e. 25 locations). If a collared wolf or its tracks were visually observed crossing a road during the monitoring session, I recorded the exact crossing location with a GPS unit. Tracks were only recorded as actual crossing locations when I could be certain that they were those of the collared wolf. During the winter of 2000/2001, I snow-tracked wolves immediately following monitoring sessions to determine the actual frequency of road crossings within the 24-hour monitoring period.

I converted wolf telemetry locations and tracking sessions to spatial GIS (Geographic Information System) files using Arcview 3.2 (ESRI Inc., Redlands, CA.), and superimposed a digital road layer of the study area onto the wolf location files.

To determine the accuracy of estimating road crossing location and frequency from telemetry conducted at increasing temporal intervals, I created subsets of my hourly telemetry database to reflect telemetry intervals of 2, 4, 6, 12 and 24 hours for each monitoring session. For example, the six-hour interval database included locations 1, 7, 13, 19, and 25, and the 12-hour interval database included locations

1, 13 and 25. Within each database, I created straight-line trajectories between consecutive telemetry locations within a given monitoring session using ArcView 3.2 GIS, and inferred a road crossing when consecutive locations occurred on opposite sides of a road.

Estimation of Road-Crossing Frequency

I counted the number of road crossings detected within each monitoring session via the snow tracking method and with the six temporal resolutions of radio telemetry, and calculated the proportion of actual crossings captured with each method. If a straight-line trajectory originated on one side of a road and terminated on the opposite side of the road, yet crossed the road multiple times as a result of road curvature, I counted only one crossing. I counted only major roads that were open to the public as shorter access roads would be automatically deleted from the analysis once distance between consecutive radio-locations increased.

Estimation of Road-Crossing Location

Using the hourly telemetry database and the five subsets of the hourly database, I estimated road-crossing locations as those points where straight-line movement trajectories intersected roads. Estimated locations were compared with actual crossing locations confirmed by visual observations of the animal or its tracks. Using ArcView 3.2, I measured the straight-line distance between each actual

crossing location and the corresponding estimated crossing location and recorded the error distance in metres. For cases where multiple crossings occurred within a 24-hour monitoring session, I used only those telemetry locations that occurred after or before the other crossing/s. As a result, only monitoring sessions with a single crossing were considered for the 24-hour telemetry interval. If a straight-line trajectory joining consecutive locations crossed a road more than once due to road curvature, the case was omitted from the analysis due to the inability to define the "estimated" crossing location. In addition, I omitted all crossings of the fenced sections of the TCH as straight-line movement paths may not be representative of approaches toward the highway, due to placement of wildlife crossing structures.

I calculated the mean and median road-crossing error distance for each of the six telemetry interval classes. Due to the non-parametric nature of the data, I compared road-crossing error associated with different telemetry intervals using a Kruskal-Wallis test (SYSTAT 10.0). I used non-parametric post-hoc multiple comparison tests to determine where differences occurred within the groups (Dunns test for unequal sample sizes) (Zar 1999).

RESULTS

Road-Crossing Frequency

A total of seventy-one telemetry-monitoring sessions and 226 road crossings were used in the road-crossing frequency analysis. Nine of the 71 sessions were partially or completely snow-tracked, revealing twenty-nine road crossings. One hundred percent of crossings detected during snow tracking were detected with hourly telemetry (n = 29). As a result, I compared the number of road crossings detected with radio-telemetry conducted at two, four, six, twelve and twenty-four hour intervals to the frequency of road crossings captured with hourly telemetry (Table 4-1). As time between consecutive radio telemetry locations increased, the number of detected road crossings decreased (Figure 4-2).

Road-Crossing Location

Only twenty-one monitoring sessions were appropriate for inclusion in the analysis of road-crossing location error. Twenty-four actual road-crossing points were used in the analysis. Due to the high number of monitoring sessions with multiple crossings, sample size decreased as time between consecutive radio locations increased. Only four data points were available for the 24-hour resolution. Median error distances associated with each temporal resolution are presented in Table 4-2. There were significant differences among error distances associated with the six temporal levels of telemetry data ($H = 18.574$; df = 5; $P =$

0.002), however post-hoc multiple comparisons produced ambiguous results, likely as a result of the low sample size.

DISCUSSION

When compared with snow-tracking data, radio-telemetry conducted at hourly intervals detected all road crossings of collared wolves. As the time interval between consecutive locations increased, the ability to detect road crossing frequency and location decreased. Road crossing locations estimated from telemetry data became less accurate as time between consecutive locations increased, however low sample size precluded the identification of statistically significant differences between temporal interval classes. My initial sample size of 226 road-crossings was reduced to only 24 for statistical analysis as a result of multiple-crossing situations, the effect of road curvature, and the inability to use the majority of TCH crossing data due to biases related to highway fencing. These numbers suggest that such data are difficult to acquire in natural systems.

Despite low sample size, there were differences in the accuracy of road-crossing locations estimated with telemetry data collected at the six different time scales, and this data can provide useful guidelines for planning road mitigation for wolves. Radio-telemetry conducted at hourly intervals best represented crossing frequency however, an inflation factor (% crossings gained with decreasing time between telemetry locations) may be used to approximate total number of

crossings from data collected at greater temporal intervals. Telemetry data collected on an hourly basis may provide the most spatially precise data for planning wildlife crossing structures, however when effort is considered, data collected at greater temporal intervals may be more efficient while still being adequate for planning crossing structures and slow speed zones. Relatively large increases in error distance occurred between the two and four hour telemetry interval, and between the 12 and 24-hour interval. Telemetry conducted every four hours is still relatively accurate at deriving estimated road crossing locations (466 m), and the error associated with the next two higher temporal interval classes does not deviate much from that of the 4 hour method (6 hour error = 585 m; 12 hour error = 623 m). If one considers the median instead of the mean for representing the central tendency of the data, the difference between these intervals further decreases. Telemetry conducted every 12 hours could yield meaningful wildlife crossing data to assist with highway mitigation. Telemetry conducted at greater intervals, such as every 24 hours, may be better suited to identify general road crossing zones for posting wildlife crossing signage and reducing speed limits.

LITERATURE CITED

Alexander, S.M. 2001. A spatial analysis of road fragmentation and linkage zones for multi-species in the Canadian Rocky Mountains: A winter ecology study. Ph.D.Dissertation. University of Calgary, Alberta. 352pp.

Callaghan, C.J. 2002. The ecology of gray wolf (*Canis lupus*) habitat use, survival and persistence in the Central Rocky Mountains, Canada. Ph.D. Dissertation. University of Guelph, Ontario. 211pp.

Clevenger, A.P. and N. Waltho. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. *Cons. Biol.* 14: 47-56.

Forman, R.T.T. 2000. Estimate of the area affected ecologically by the road system in the United States. *Cons. Biol.* 14: 31-35.

Gibeau, M.L. 2000. A conservation biology approach to management of grizzly bears in Banff National Park, Alberta. Ph.D Dissertation, University of Calgary, Alberta.

Cornwell, L., C. Pacas and J. Green. 1996. Introduction: Ecological Outlooks for the Banff Bow Valley. Chapter 1 in: Green, J., C. Pacas, L. Cornwell and S. Bayley (eds). Ecological Outlooks Project. A Cumulative Effects Assessment and Futures Outlook of the Banff Bow Valley. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, ON. 20 pp.

Hebblewhite, M. 2000. Wolf and elk predator-prey dynamics in Banff National Park. M.Sc. Thesis. University of Montana. 130 pp.

Jaeger, J.A.G. and L. Fahrig. 2002. Modeling the effects of road network patterns on population persistence: relative importance of traffic mortality and 'fence effect'. *Proceed. Int. Conf. on Ecol. and Transport*. 2001. p. 298-312.

Paquet, P.C., J. Wierzchowski, and C. Callaghan. 1996. Effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 in: Green, J., C. Pacas, S. Bayley and L. Cornwell (eds.). A cumulative effects assessment and futures outlook for the Banff Bow Valley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa, ON. 74pp.

Serrouya, R. 1999. Permeability of the Trans Canada Highway to black bear movements in the Bow Valley of Banff National Park. MSc. Thesis University of British Columbia.

White, G.C. and R.A. Garrott. 1990. Analysis of Wildlife Radio Tracking Data. Academic Press Inc. 383 pp.

Zar, J.H. 1999. Biostatistical Analysis. Fourth Edition. Prentice-Hall Inc. New Jersey.

Table 4-1: Number of wolf road crossings detected with six temporal resolutions of radio-telemetry and the proportion of hourly road crossings detected at each subsequent resolution.

Telemetry Interval (hrs)	# Crossings Detected	% of Hourly Crossings Detected
1	226	100
2	177	78.3
4	147	65
6	121	53.5
12	99	43.8
24	73	32.3

Table 4-2: Median and mean error (m) of wolf road crossing locations estimated from radio telemetry conducted at six temporal intervals.

Telemetry Interval (hrs)	n	Median Error (m)	Mean Error (m)
1	21	61	152
2	23	168	230
4	18	232	466
6	15	302	585
12	12	297	623
24	4	803	878

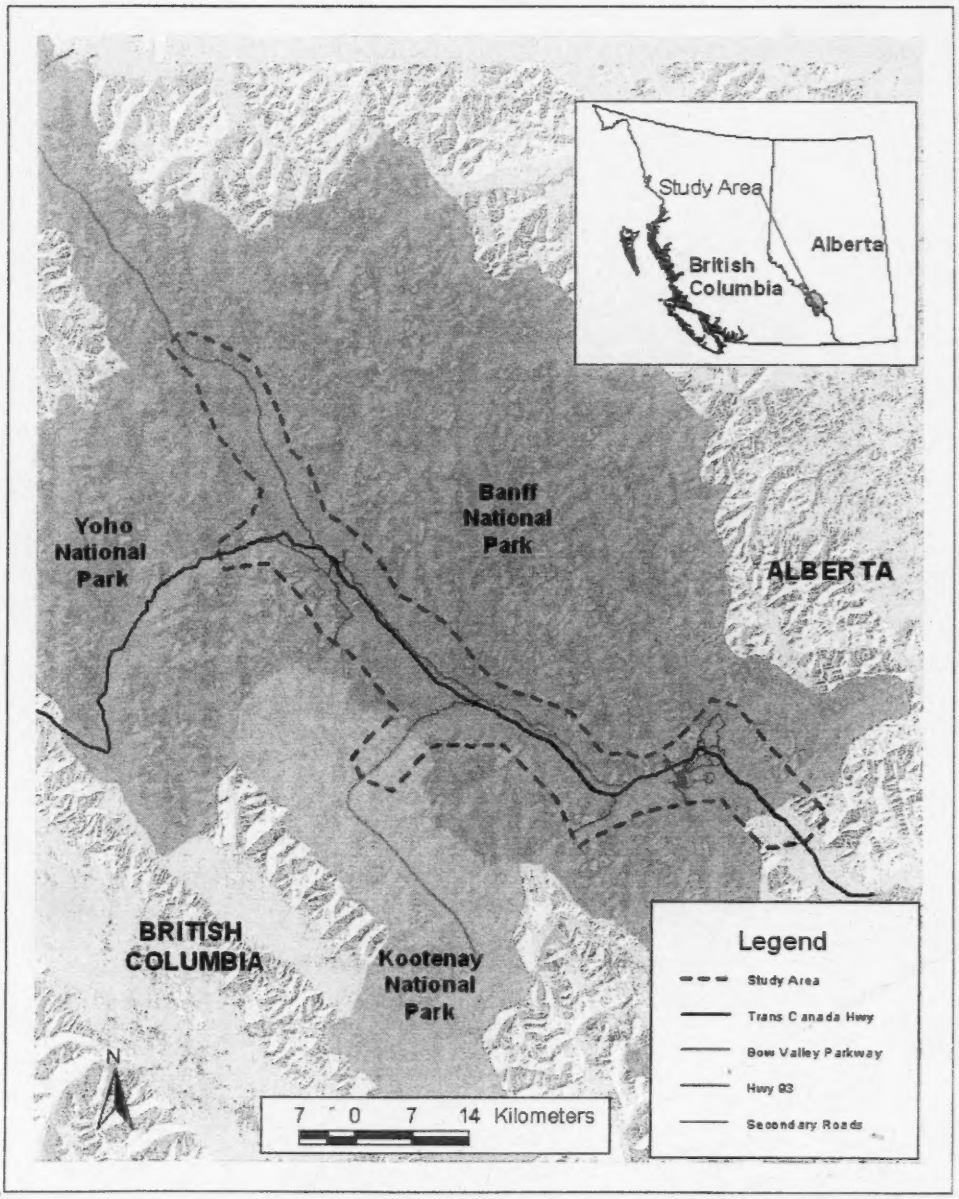

Figure 4-1: The greater Banff National Park region illustrating the study area.

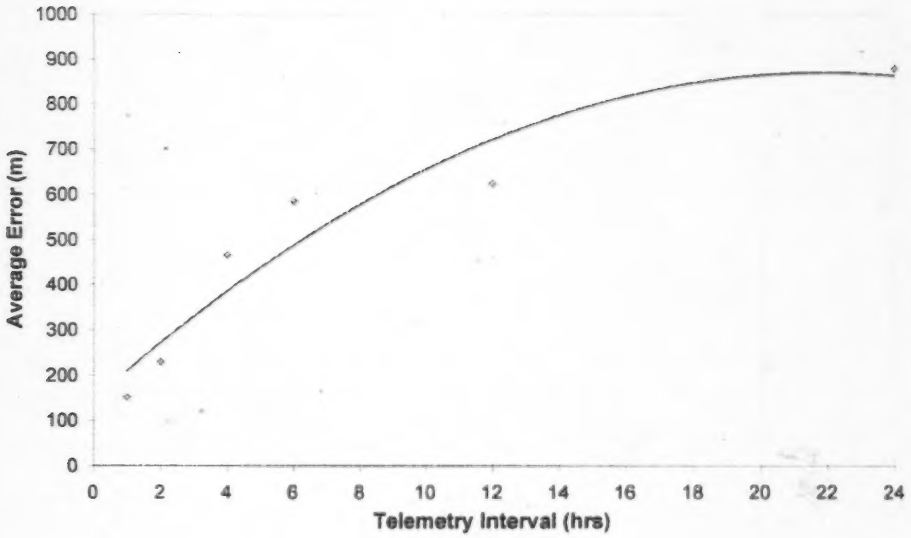

Figure 4-2: Mean error distance (m) of road crossing locations estimated with radio-telemetry conducted at increasing temporal intervals.

CHAPTER 5

GENERAL CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

My results suggest that wolves, black bears and grizzly bears may use temporal spacing to access or move across areas of high human-use to varying degrees. Two wolves dramatically shifted their movement and road-crossing patterns from predominantly diurnal and crepuscular in winter, to predominantly nocturnal and crepuscular during summer when human use of the Bow Valley is high. In winter, despite their largely diurnal and crepuscular movement pattern, wolves used nocturnal hours to move through areas of high human-use. Wolves used wildlife corridors throughout the day and night, lending support to the restriction of human use of corridors. Although black and grizzly bears moved and crossed roads primarily during daylight and crepuscular hours, evidence suggests that this pattern may be related to the connection between sightability and optimal foraging (Garshelis and Pelton 1980; Lariviere et al. 1994; Reimchen 1998). Crepuscular and night activity was documented in both black and grizzly bears when navigating through areas of high human-use or through wildlife corridors. It is important to note that I documented only habituated grizzly bears using wildlife corridors and habitat adjacent to areas of high human-use. Sample size of both wary (n = 1) and habituated grizzly bears (n = 2) was low.

All three species increased their use of one or more spatial security features (vegetative security cover, road curvature, terrain roughness) at crossing sites of the Bow Valley Parkway during periods of high traffic volume, indicating a loss of habitat effectiveness and a temporal reduction in road permeability. This pattern suggests that current traffic levels on the Bow Valley Parkway are reducing habitat effectiveness for large carnivores.

Monitoring road-crossing frequency of large carnivores over time may assist in identifying changes in landscape permeability and relative risk of mortality for these wide-ranging mammals. I found that telemetry conducted every one to twelve hours may be most efficient for estimating wolf road-crossing frequency and location, while telemetry conducted at greater intervals may be better suited to estimate more general road-crossing and linkage zones.

In conclusion, increasing levels of human use in the Bow Valley of Banff National Park threaten the ability of the region to support large carnivore populations. Parks Canada must more actively manage human use of the landscape to restore habitat security for wolves, black bears and grizzly bears. Based on the results of this research, I recommend the following:

1. Implementation of <u>mandatory</u> temporal road closures along secondary roads to provide wolves, black bears and grizzly bears with secure road-crossing opportunities and free movement during active periods. Specifically, I

recommend that the BVP be closed to all forms of human travel with a locked gate between 17:00 and noon throughout the year. I recommend that the temporal closure of the BVP extend from Banff to Castle Junction, in order to protect a wolf denning area and important spring and summer black and grizzly bear habitat.

2. Limit human activity to daylight hours in all areas outside of town limits and the footprints of campgrounds and Outlying Commercial Accommodation's (OCA's). The TCH and CPR should be exempt from this limitation.

3. Discourage off-trail recreational activity in important carnivore habitat (e.g. the montane ecoregion) to ensure that diurnal wildlife movements are not interrupted by spatially unpredictable disturbances. Restrict casual and organised (i.e.eco-tourism groups) recreation to using only existing trails for both summer and winter activities (e.g. hiking and snowshoeing).

4. Limit human use of wildlife corridors throughout all hours of the day and night to maintain habitat effectiveness of these important linkage zones and to allow for unimpeded movement of wary species.

5. Prohibit further development of new or existing facilities aimed at increasing human use of the BVP or adjacent habitat. Failure to do so may further decrease habitat effectiveness for large carnivores in this area.

LITERATURE CITED

Garshelis, D.L., and M.R. Pelton. 1980. Activity of black bears in the Great Smoky Mountains National Park. *J. Mamm.* 61(1): 8-19.

Lariviere, S., J. Huot, and C. Samson. 1994. Daily activity patterns of female black bears in a northern mixed-forest environment. *J. Mamm.* 75(3):613 - 620.

Reimchen, T.E. 1998. Diurnal and nocturnal behavior of black bears, *Ursus americanus*, on bear trails. *Canadian Field-Naturalist* 112(4): 698-699.